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Nouveaux Types de Bouteilles à Eau en Verre et leur Emploi en Océanographie, en Limnologie et en Bactériologie

Par

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Le progrès remarquable de la chimie océanographique pendant les dernières années, avec l'application de réactions extrêmement sensibles, a exigé l'usage d'appareils où les échantillons d'eau qui sont prélevés aux différentes profondeurs ne doivent pas être au contact des métaux. On sait déjà bien que toutes les *bouteilles à eau* sont construites en métal, d'habitude en bronze et pour certaines déterminations le contact de l'eau marine avec la surface métallique peut en altérer le contenu, spécialement par rapport aux concentrations bien faibles en éléments oligodynamiques.

Déjà les bactériologues avaient adopté, il y a quelque temps, de petits récipients en verre, fixés à la flamme, stérilisés, qu'on enfonce dans l'eau et avec lesquels on recueille, après la rupture de l'extrémité fixée, un petit échantillon d'eau. Ce dispositif, par example le modèle Sclavo (il y en a aussi d'autres: Fischer, Siebert, etc.) a trouvé une remarquable application dans les recherches d'eau douce, utilisée surtout pour les aqueducs ou bien dans les analyses bactériologiques des eaux minérales de table.

Mais en mer ce système ne peut pas être utilisé parce que les petits tubes, à cause de leurs parois trop minces, ne resistent pas aux fortes pression que l'on rencontre aussi dans les profondeurs modérées.

Pour prévenir d'inconvénient, plusieurs bouteilles ont été garnies d'un revêtement de verre qui pourtant n'exclut pas complètement le contact métallique, surtout dans les couvercles, même s'ils sont recouverts d'un bouchon en caoutchouc.

Au Musée Océanographique de la Principauté de Monaco on construit des hydrophores en matériaux plastiques. Mais au point de vue chimique, je pense qu'il y a lieu de préférer le verre, car il est notoire que les résines synthétiques peuvent facilement jouer le rôle de sélecteurs d'ions, soit par échange soit par adsorption directe. Dans ce cas il est possible aussi que des éléments oligodynamiques soient éliminés complètement de l'échantillon, bien plus facilement que cela ne se produirait avec les récipients en verre, d'autant plus que dans ceux-ci aussi les solutions extrêmement diluées peuvent subir des variations dans leur concentration, par suite de l'action de surface.

Pendant les recherches méticuleuses effectuées depuis longtemps dans le

laboratoire de l'Institut Expérimental Thalassographique de Trieste pour une détermination du cuivre biologique et marin, on a préparé — dans un but de contrôle — des solutions très diluées de sulfate de cuivre, à la concentration de peu de gamma/litre. De telles solutions sont toujours employées pour contrôler la méthode bien connue de détermination du cuivre usée dans notre Institut.

On a remarqué, à présent, qu'il y a des verres qui, quelquefois, atténuent la concentration du cuivre, tandis que d'autres la laissent presque inaltérée. La perte en titre des solutions, relevée par la spectrophotométrie, correspond, presque exactement, au cuivre qu'on peut obtenir des parois du récipient: —

(1) s'il a été soigneusement vidé de la solution et bien convenablement rincé avec de l'eau distillée;

(2) en y introduisant quelque ml de 2 n HNO_3 et en portant la solution de nouveau à la détermination cuprique-spectrophotométrique.

Ce contenu de cuivre est la partie qui reste adsorbée aux parois du récipient pendant la première opération. Il faut alors que les grands flacons employés soient lavés avec de l'eau distillée deux fois et traités de nouveau avec quelques ml de 2 n HNO_3, qui doivent être unis à la première solution.

La description de ces hydrobouteilles a été déjà faite dans plusieurs publications et surtout dans tous les traités modernes d'océanographie, auxquels nous vous renvoyons pour la description des détails et pour la bibliographie, de laquelle ZOBELL nous donne un très bon résumé dans sa publication de 1941.

Nous voulons indiquer ici seulement quelques uns des travaux les plus remarquables concernant ces études.

PORTIER et RICHARD (1907) ont décrit une méthode pour recueillir des échantillons d'eau pendant des recherches bactériologiques avec une ampoule cylindrique de verre, vide, stérilisée à 120°C et introduite dans une boîte métallique qui en se renversant brise la pointe de l'ampoule en verre.

Pour la croisière atlantique du "Meteor", entre les autres instruments, il y avait aussi des bouteilles terminales imaginées par MERZ et construites dans les usines Marx et Berndt de Berlin. Leur capacité de 4000 ml consentait le prélèvement d'un remarquable volume d'eau par le moyen d'une seule opération. Dans l'intérieur de la bouteille il y avait un cylindre en verre, à paroi épaisse, avec une fermeture inférieure et une supérieure en caoutchouc. Les robinets de prélèvement sont aussi en caoutchouc durci, pour éviter le contact de l'eau, qu'on a recueillie, avec les parois métalliques et obtenir des expériences chimiques-analytiques de précision sur des éléments rares.

Aussi Claude E. ZOBELL (1941 a & b), dans ses études sur la bactériologie marine, a projeté divers systèmes pour recueillir l'eau dans un récipient stérile à une grande profondeur, en évitant toujours les contacts métalliques.

SPILHAUS et MILLER (1948) ont modifié le bathythermographe, en y ajoutant onze récipients disposés circulairement et adhérents à l'extérieur, avec une fermeture auto-fonctionnante pendant l'immersion, et aussi lorsque le navire est en mouvement.

AABYE JENSEN et STEEMANN NIELSEN (1952) ont employé un récipient en verre de 500 ml avec robinetterie aussi en verre, qu'ils pouvaient manoeuvrer à travers un engin métallique avec l'envoi de plombs (messagers).

La "bouteille à eau" de FJARLIE (1953) ressemble à celle construite par EKMAN, mais avec l'avantage d'un plus prompt échange entre l'eau qui est dedans et celle du milieu.

SELLERIO (1954) a construit un support complexe en fonction électromagnétique auquel est soudée, par son cou, une simple bouteille, fermé avec un bouchon ordinaire en caoutchouc. Le bouchon est commandé par le noyau mobile de l'électro-aimant, alimenté à travers le câble de suspension de l'appareil.

Pour la même raison aussi THOMPSON et CHOW (1955) ont construit une bouteille constituée essentiellement d'un cylindre de Lucite, d'une capacité de 1750 ml et commandée par un messager qui en détermine le remplissage à la profondeur désirée.

Au cours des études récentes sur les concentrations de quelques *éléments oligodynamiques* présents dans la mer, et surtout du cuivre — études qui ont eu lieu à l'Institut Thalassographique de Trieste — on a reconnu inopportun pour les échantillons qui doivent être utilisés à ce propos, de les recueillir dans des récipients en bronze, qui provoquent un contact, plus ou moins long, avec un alliage de cuivre.

Et c'est pour cela qu'on a dû trouver un système qui permet de prélever un volume d'eau — près de 500/600 ml et à grande profondeur, — dans des tubes en verre spécial: pyrex, Murano ou une autre qualité bien choisie et résistante. Ces tubes, si on les utilise pour des profondeurs plus grandes que 500 m, doivent avoir les parois bien solides et alors leur diamètre résulte légèrement réduit.

Les premiers essais avec ce système furent effectués dans l'Adriatique, où les profondeurs ne sont pas excessives et où les tubes ont résisté assez bien jusqu'aux plus grandes profondeurs, qui dans l'Adriatique méridionale ne surpassent pas les 1200 mètres.

Au cours des immersions il arrive quelquefois, si les tubes n'ont pas les parois parfaitement régulières, qu'ils soient écrasés par la pression environnante.

Avant leur usage, les flacons sont soumis dans le laboratoire à une préparation très soignée. Ils doivent être bien lavés nombre de fois, dans une eau distillée, pour être sûr qu'il n'est pas resté de sels adhérant à leurs parois. Ensuite le vide s'y forme.

Pour les tubes il suffit d'extraire l'air avec une pompe ordinaire roulante à huile, sans besoin d'obtenir un vide trop excessif. L'extrémité du flacon est fermée à la flamme et cette opération est assez facile après quelques expériences. Alors, tout est prêt à l'usage; on l'adapte au fût — qui est reproduit dans la Figure 1 — et on l'immerge à la profondeur désirée. En faisant glisser un messager assez pesant le long d'un fil, il heurte le levier horizontal qui transmet le mouvement à l'intérieur et qui cause la rupture de l'extrémité de la bouteille. L'eau y entre avec violence et remplit très rapidement le tube.

Lorsque l'appareil est remonté à la surface, on enlève la bouteille d'eau et il faut fermer l'extrémité supérieure avec un petit morceau de tube en caoutchouc, tandis que l'autre extrémité doit être aussi fermée, mais avec un petit tube en verre. C'est ainsi que l'échantillon recueilli est bien gardé pour l'analyse en laboratoire, parce que l'eau contenue n'est pas venue au contact des parties métalliques.

Le même appareil a été employé aussi pour recueillir des échantillons pour l'analyse des *gaz dissous*. Le flacon est, dans ce cas, inséré sur la tige en position inverse, c'est-à-dire avec la pointe au-dessous et naturellement aussi la tige à la partie mécanique de rupture disposée autrement. La manière de fonctionner paraît clairement dans la Figure 2. Mais pour ces mesures la préparation des bouteilles est un peu différente. Les gaz contenus dans l'eau marine son

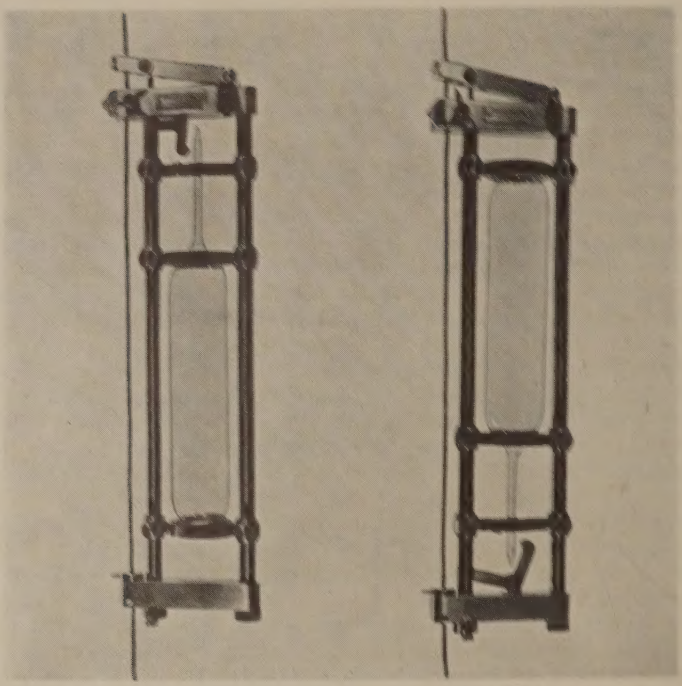


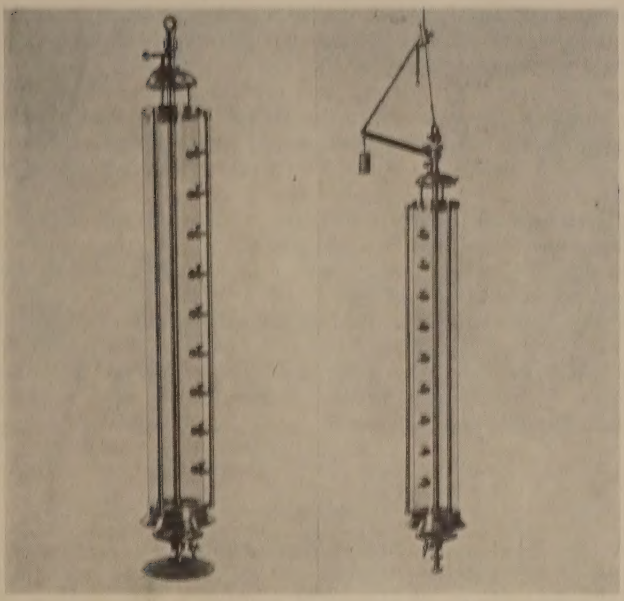
Fig. 1 Fig. 2

Figure 1. Flacon fermé à la flamme inséré sur la tige.
Figure 2. Flacon fermé à la flamme inséré sur la tige en position inverse.

égaux, à l'analyse, à ceux de l'air atmosphérique et pour cela il est nécessaire d'éviter qu'ils soient présents au dedans, aussi en le plus petit peu, avant l'usage. Et pour cela aussi avant cette opération le flacon doit être soigneusement nettoyé pour y obtenir le vide. Il est rempli plusieurs fois d'hydrogène, de manière qu'après 3 ou 4 remplissages on peut considérer disparus tous les résidus d'air et il y reste seulement une quantité très légère d'hydrogène, en relation avec la pression résiduelle.

Dans les analyses suivantes des gaz, puisque l'hydrogène n'est pas contenu dans l'air à la surface de la mer, sa présence éventuelle dans la bouteille est due à la manière peu soignée de sa préparation.

Naturellement, autant les flacons avec l'ouverture en haut que le dispositif pour recueillir des échantillons en vue de l'analyse des gaz dissous — qui à la pointe de rupture du verre dirigée vers le bas — peuvent être employés aussi pour recueillir l'eau qui peut être nécessaire pour l'étude bactériologique. Dans ce cas, les flacons soigneusement préparés selon les deux techniques décrites auparavant, doivent être encore soumis à une très diligente stérilisation avec une longue permanence dans un thermostat, à température toujours au dessus des 100° C.



(a) (b)

Figure 3. (a) Bouteille à eau en plexiglass, avec 10 robinets, pour le prélèvement de l'eau par couches. (b) La même bouteille avec un dispositif additionnel.

Pendant des recherches thalassographiques récentes, ces deux applications, soit pour recueillir des échantillons d'eau, soit pour analyser des gaz dissous, ont donné de très remarquables résultats.

Le progrès de l'étude des sédiments du fond marin a conseillé le contrôle du contenu en oxygène de la couche d'eau immédiatement au-dessus du fond.

Avec les bouteilles ordinaires Ekman et Nansen, il est difficile de pouvoir recueillir des échantillons à un bref espace l'un de l'autre. EKMAN donne des échantillons à 1 mètre de hauteur sur le fond et éventuellement, lorsque la profondeur n'est pas trop considérable, aussi jusqu'à $\frac{1}{2}$ mètre. Pour cela on peut avoir seulement 3 échantillons au voisinage du fond, avec ceux qu'on peut tirer à l'aide d'une bouteille qui traîne sur le fond.

Alors, devant relever la stratification de l'oxygénation de l'eau en toute proximité du fond, j'ai retenu nécessaire de construire une bouteille avec un cylindre en plexiglass, bien résistant, avec 10 petits robinets latéraux, qui permet le prélèvement de l'eau par couches, tout près les unes des autres. On plonge l'hydrobouteille lentement, afin que l'échange de l'eau dans son intérieur arrive sans mélanges (Fig. 3a).

Le mouvement doit être ralenti surtout au voisinage du fond, jusqu'à ce que le disque inférieur, au contact du fond, fasse déclencher les deux couvercles de fermeture et que la bouteille revienne à la surface en apportant environ 15 litres d'eau.

Par la méthode Winkler, employée pour la détermination de l'oxygène et en

opérant de haut en bas, on obtient, par ordre, des données analytiques relatives à une stratification d'environ 10/12 cm, de 1 mètre de hauteur, en toute proximité du fond marin.

Dans les recherches adriatiques, cette méthode a donné des résultats très utiles, parce qu'on a pu relever constamment l'allure de l'oxygénation et son décroissement vers le fond, particulièrement lorsque sa surface a un caractère réductif, où l'eau marine, au contact du sédiment, est complètement privée d'oxygène.

Avec un dispositif additionnel, illustré par la Figure 3b, on démontre la possibilité d'employer cette bouteille à une profondeur quelconque, même loin du fond de la mer. On arrive alors à porter à la surface, au moyen d'une seule opération, à peu près 15 litres d'eau.

Cela va sans dire que la bouteille doit être suspendue à l'extrémité du câble en acier et qu'elle peut être employée pour des mesures en séries avec d'autres bouteilles, fixées plus haut, mais à des hauteurs diverses, en faisant bien attention d'ajouter au dernier hydrophore Ekman ou Nansen le messager qui convient à la bouteille géante du fond.

Résumé

Les réactions chimiques employées aujourd'hui en colorimétrie et en spectrophotométrie sont tellement sensibles ce qui permets la détermination des éléments oligodynamiques contenus non seulement dans l'eau de mer mais aussi dans l'eau douce.

Puisque telles déterminations sont très importantes pour la biologie, les recherches dans ce secteur seront intensifiées de plus en plus.

L'usage d'une bouteille à reversement métallique présente un inconvenient très sérieux, car, dû à l'éffet du métal avec lequel le recipient de récolte est construit, l'eau sera facilement pollué.

Pour cette raison l'auteur l'a juge opportun de remplacer le métal par le verre et il a ensuite fait construire des flacons cylindriques, dans lesquels on a fait le vide, et qui seront plongés dans l'eau à la profondeur désirée, par une tige expressément construite. Le remplissage des flacons se fait par la chute d'un messager ordinaire.

Pour le prélèvement des échantillons d'eau tout près du fond de la mer et jusqu'à 1 m de celui-ci, une bouteille géante a été construite, permettant la récolte de 10 échantillons à une distance de 10 cm l'un de l'autre.

Summary

The chemical reactions employed to-day in colorimetry and spectrophotometry, are so sensitive that the determination of oligodynamic elements in sea water as well as in fresh water, is now possible.

Such determinations are very important from the view point of biology and therefore the researches in this field are widely increasing.

The use of metallic bottles for the collection of water samples for the determination of oligodynamic elements, presents a serious inconvenience, because the water may very easily be polluted by contact with the metal.

For this reason the author has substituted the metal with glass, and has made a cylindric bottle which, after being emptied for air, is lowered to the desired depth, by means of a suitable support. The filling of the bottle is produced by an ordinary messenger.

For the collection of water samples near the sea floor and up to 1 m from it, a giant bottle has been constructed by which it is possible to collect 10 samples at a distance of 10 cm from each other.

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Pour ceux qui puissent avoir de l'intérêt à une bibliographie complète, il sera tout facilement possible l'obtenir avec les oeuvres citées.

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Appareillage Employé en Méditerranée pour l'Etude de la Production de Matière Organique

Par

Jean Brouardel et Emile Rinck

Introduction

La production de matière organique en Méditerranée, par la méthode du ^{14}C a commencé à être étudiée par nous à une première station située à proximité de Monaco (BROUARDEL et RINCK, 1956).

La méthode employée est celle du Professeur STEEMANN NIELSEN de Copenhague; l'appareillage a cependant été modifié pour l'adapter aux conditions méditerranéennes, et c'est sa description qui fait l'objet de cette note.

Boîte pour Cellule Photoélectrique

Les mesures photoélectriques ont été faites avec des cellules de Lange de 7,5 cm de diamètre, analogues à celles dont se sert STEEMANN NIELSEN; cependant, les boîtes étanches employées par l'auteur danois n'ont pu être retenues. En effet, en raison de la plus grande pénétration de la lumière dans les eaux méditerranéennes, ces boîtes devaient être descendues à des profondeurs bien supérieures à 100 m, pour lesquelles l'étanchéité n'était plus maintenue et où même l'écrasement du verre se produisait.

Aussi avons nous réalisé le dispositif (Figure 1) pour lequel, en raison de l'absence de tout espace vide, ni écrasement ni pénétration de l'eau n'est possible.

La boîte elle même est constituée par un bloc d'afcodur (chlorure de polyvinyle rigide) sur lequel repose le disque sensible de la cellule, recouvert d'une plaque circulaire de plexiglass de même diamètre et de 1 cm d'épaisseur. Un joint assure la sortie du conducteur, dont les deux fils noyés dans l'afcodur assurent le contact avec les deux surfaces de la cellule.

Trois tiges, de 1 m de long chacune, étaient fixées perpendiculairement à l'axe de la boîte et leurs extrémités étaient reliées au câble par une patte d'oie suivant le dispositif employé par STEEMANN NIELSEN.

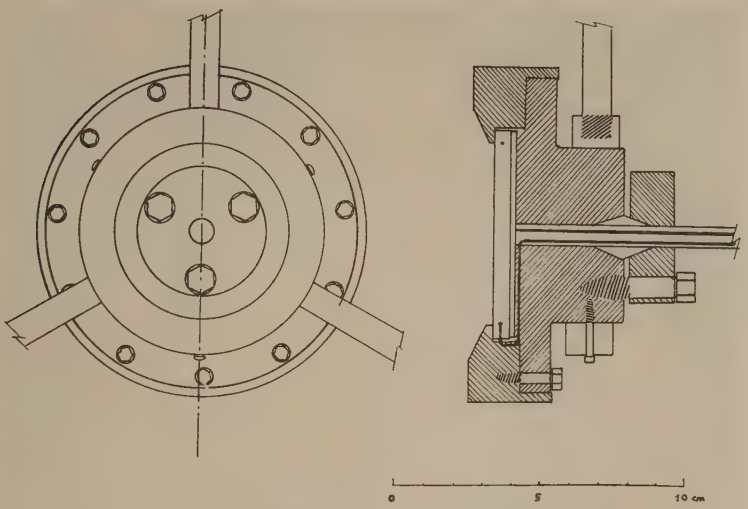

Figure 1. Boîte étanche pour cellule photoélectrique.

Bouteilles de Prélèvement

Les bouteilles de prélèvement classiques, Nansen, Knudsen, etc. nous ont, ainsi qu'aux autres auteurs, semblé peu favorables pour les prélèvements particuliers destinés à ces recherches, en raison de leur construction entièrement métallique.

Nous avons également éliminé les bouteilles à vide en raison de la dégazéification quasi instantanée qui se produit dans l'échantillon d'eau au moment du remplissage. L'expérience a montré que les gaz libérés ne se redissolvent que très lentement dans l'eau, dont la composition est ainsi profondément modifiée. Par ailleurs, en raison de la difficulté de réalisation technique de ces bouteilles et en particulier de l'étanchéité défectueuse et incontrôlable des robinets au delà d'une certaine profondeur, nous avons été conduits à les abandonner.

Dans ces conditions nous avons réalisé des bouteilles de prélèvement qui permettent d'échapper à ces inconvénients.

1. Bouteille plexiglass

Elle se compose d'un tube en plexiglass de 50 cm de long et de 60 mm de diamètre extérieur, permettant de faire des prélèvements d'eau de l'ordre de 1 litre. Ce tube est supporté par un bâti en acier inoxydable sur lequel les clapets d'obturation sont fixés, ainsi que le mécanisme de déclenchement et le porte-thermomètres.

L'appareil est maintenu sur le câble du treuil, à la partie supérieure, par une "serre câble" à écrou à oreilles et à la partie inférieure par une "queue de cochon".

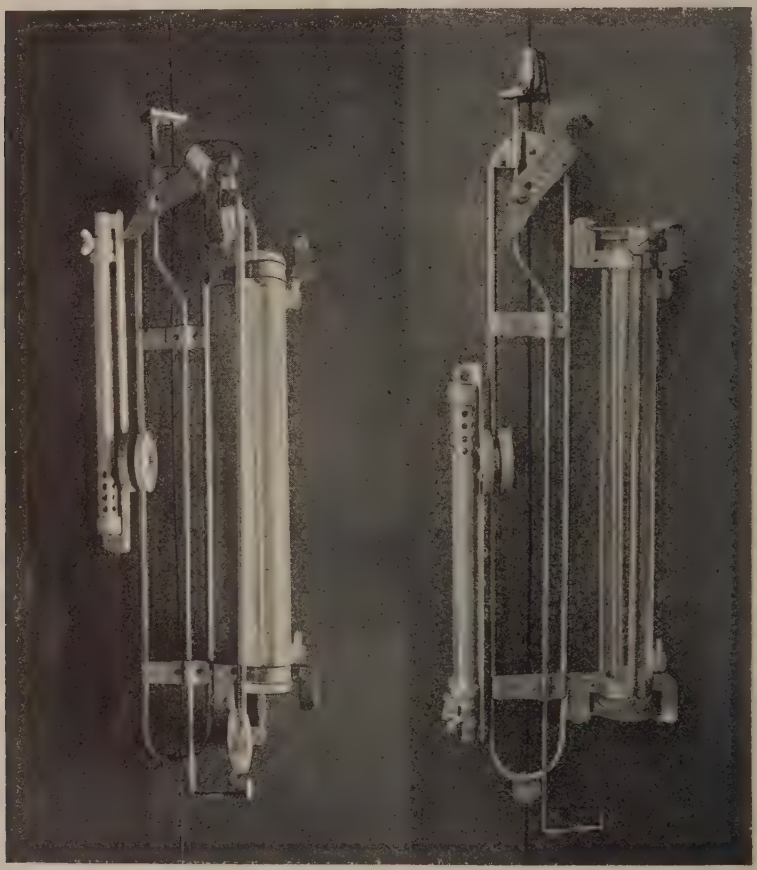

Figure 2. Bouteille de prélèvement, à la descente, clapets ouverts.

Figure 3. Bouteille de prélèvement après déclenchement par messager.

A la descente (Figure 2), la circulation de l'eau se fait librement dans le tube dont les deux clapets, enclenchés dans des ergots, sont maintenus ouverts.

L'appareil descendu à la profondeur désirée est déclenché par messager (Figure 3). Celui ci, en percutant la tige centrale, provoque son abaissement et libère simultanément les clapets qui sont entraînés par deux puissants ressorts. Le clapet inférieur est libéré par action directe de la tige, le clapet supérieur par intermédiaire d'une pièce à came en forme d'S.

En même temps, le porte-thermomètres est libéré et se renverse en pivotant autour d'un axe, avec les thermomètres qu'il contient.

Plusieurs de ces bouteilles peuvent être utilisées simultanément sur le même câble, la poulie servant d'axe au porte-thermomètres pouvant porter un messager qui se libère au moment du pivotement.

Après remontée de la bouteille, les prises d'eau se font par deux robinets en plexiglass fixés à demeure sur le tube.

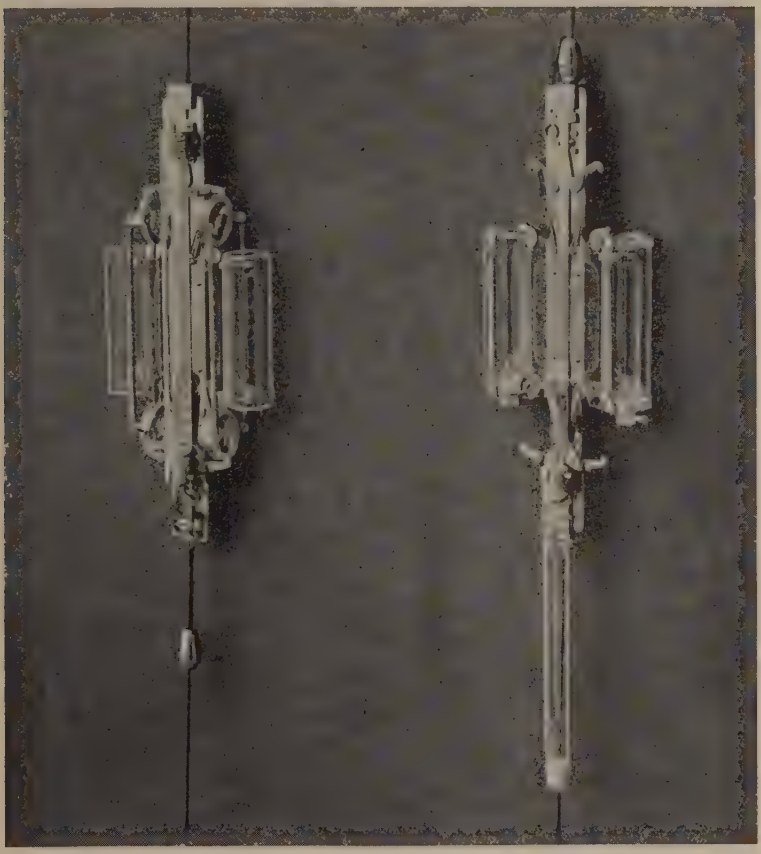

Figure 4. Appareil automatique, à la descente.

Figure 5. Appareil automatique après déclenchement.

Ces prises sont transvasées dans des flacons de 170 ml auxquelles on ajoute le contenu d'ampoules de $NaH^{14}CO_3$. Après remplissage, ces flacons sont fermés par des capsules de caoutchouc, puis fixés le long d'un filin accroché à un radeau et redescendus à la profondeur de prélèvement de l'eau qu'ils contiennent. Ils y sont exposés pendant une demi-journée solaire. Aussitôt après exposition, les flacons remontés, leur contenu est filtré sur des membranes de collodion. Ces dernières opérations se font suivant la méthode de STEEMANN NIELSEN.

A la suite des premières expériences effectuées suivant ce mode opératoire, nous avons cherché à simplifier les opérations par l'emploi d'un appareil automatique permettant: la prise d'eau, le marquage au ^{14}C dans l'appareil lui même et à la profondeur de prise, le mélange de la solution radioactive avec l'échantillon d'eau, l'exposition et enfin, après remontée, la filtration.

Dans ce but nous avons réalisé la bouteille automatique suivante.

Figure 6. Filtration à partir de l'appareil automatique, clapets inférieurs bloqués.

2. Bouteille automatique

L'appareil se compose essentiellement de deux tubes de plexiglass de 16 cm de long et de 50 mm de diamètre extérieur faisant des prélèvements de 250 ml chacun.

Ces deux tubes sont reliés par des ailerons de plexiglass à une plaque mince en bronze phosphoreux chromé. Sur cette plaque est fixée une tige qui, percutée par un messager, libère simultanément les quatre clapets, le porte-thermomètres et un autre messager qui déclenchera la bouteille suivante. Douze appareils de ce genre peuvent en effet être utilisés simultanément sur le même câble.

L'appareil en position de descente (clapets ouverts) est figuré en Figure 4, et après déclenchement en Figure 5.

Marquage au ^{14}C. – La solution radioactive est contenue dans de petites ampoules de 1 ml en verre mince. Avant l'expérience, les ampoules, dont on a coupé l'alèse, sont recouvertes d'un court et mince capuchon de caoutchouc qui permettra l'équilibre des pressions et empêchera donc le bris prématuré de l'ampoule quelle que soit la profondeur à laquelle on la descendra.

Sur le clapet supérieur est fixé une agrafe de plexiglass qui reçoit l'ampoule ainsi préparée.

Lors de l'action du messager, le clapet porte-ampoule est libéré, et en fin de course l'ampoule vient se briser sur trois petites dents d'acier inoxydable fixées à l'intérieur du tube.

Brassage. – Une fois l'ampoule brisée, les fragments de verre qui tombent à l'intérieur du tube commencent déja à mélanger la solution radioactive à l'eau prélevée. Simultanément, pour parfaire ce mélange, l'action du clapet inférieur intervient. Un élastique a été tendu entre les dents du casse-ampoule situé à la partie supérieure du tube, et une petite pièce en plexiglass à la partie inférieure. Cet élastique, porteur d'une hélice en plexiglass a été vrillé avant expérience et le petit moteur ainsi constitué reste bandé lors de la descente de l'appareil, l'hélice étant bloquée par un téton. La fermeture du clapet inférieur provoque le retrait du téton et libère l'hélice qui brasse l'eau à l'intérieur du tube clos. Des essais faits avec des solutions colorées ont montré l'efficacité de ce mode de brassage.

Exposition. – Après avoir amarré à un radeau le filin porteur des appareils, ceux ci restent exposés à la lumière du jour pendant une demi-journée solaire. Signalons que tout l'ensemble de l'appareil est en plexiglass, parfaitement transparent, à l'exception naturellement des ressorts de clapets, de la tige de déclenchement et de la plaque support. Ces éléments opaques sont minces et en raison de leur disposition, l'ombre portée est négligeable.

Filtration. – (Figure 6.) Après remontée, les appareils sont disposés, trois par trois, sur des plaques support qui les maintiennent verticaux. Après avoir bloqué les clapets inférieurs par un dispositif, visible sur la Figure 6, qui assure leur étanchéité, on enlève les ressorts et les clapets supérieurs.

Chacun des clapets inférieurs est en forme de verre de montre pour permettre, par lavage, une facile récupération de tous les éléments phytoplanctoniques. Le robinet du clapet est alors branché sur un tube et permet la filtration classique de Steemann Nielsen sur membrane de collodion (Fig. 6).

Résultats

Les premiers essais, en parallèle, ont montré que les chiffres de production obtenus avec ces appareils semblent être toujours très supérieurs à ceux qui résultent de l'emploi de la méthode classique. Ces différences peuvent être dues au fait que les manipulations délicates se font toutes *in situ*.

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Thermocline Topography, Zooplankton Standing Crop, and Mechanisms of Fertilization in the Eastern Tropical Pacific

By

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Introduction

A fishery will be successful only if a concentration of fish can be found in a restricted area. Nevertheless, it is very difficult to determine the factors which lead to such aggregation (cf. Fleming and Lafvasti, 1956). In regions of higher latitude, the feeding habits, migration, and reproductive cycle of fish are closely connected with the seasonal changes of meteorological and hydrographical conditions. Though the latter are complex and variable in time and space, a number of investigators have found good correlations between commercial catches and such factors as temperature, nutrient content, and precipitation (see Dietrich and Kalle, 1957, pp. 230–33; Tait, 1952; Sverdrup, Johnson, and Fleming, 1955, p. 762). Frequently these factors govern the phytoplankton production which is responsible for a rich food supply in certain areas, causing fish aggregation. Sometimes, however, in inshore waters where strong gradients exist and observation points are closely spaced, it is possible to show a direct dependence of fish behaviour (e.g., spawning, migration) upon salinity and temperature (Brandhorst, 1955; 1956).

It has been shown in the central Pacific, that tunas occur most frequently in the upwelling region along the equator with relatively high plankton standing crop (Cromwell, 1953; King and Demond, 1953; Sette, 1955). The purpose of this study is to point out the centres of high zooplankton standing crop in the eastern tropical Pacific, some of which are good tuna fishing areas; and to suggest how these rich crops can be accounted for by hydrographic factors.

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Thermocline depth and zooplankton distribution

In most regions in low latitudes a strong thermocline is found throughout the year. One result of this stratification is that the replenishment of nutrients from below to the upper lighted zone is impeded. Only by processes which change the structure of, or reduce the depth of the thermocline can nutrients in offshore waters be made available for plant production. Nutrients may be brought to the surface by upwelling; in areas where this occurs the thermocline is weakened. Nutrients may also be introduced into the surface layer where a thermocline sometimes "outcrops", or is sufficiently near the surface to allow mixing of nutrient-rich water into the shallow surface layer. Conditions are also favourable if the compensation depth for phytoplankton photosynthesis is located below the top of the thermocline; then a photosynthetically productive zone may exist in water, richer in nutrients, in and below the thermocline.

Over large areas in the eastern tropical Pacific, the thermocline is found at relatively shallow depths (c. 20–50 m), and therefore nutrients are likely to be readily available for plant production. According to Steemann Nielsen (1955) production in the tropical oceans is limited mainly by the nutrient supply. Variations in transparency of the water may also effect the available radiation and, hence, the depth of compensation and the production rate. In most regions, however, this factor seems to be less important than the available supply of nutrients. Hentschel and Wattenberg (1930) were able to correlate directly plankton and phosphate data from the South Atlantic Ocean. In the eastern tropical Pacific there are not enough phosphate data available to make such a study. However, if the supply of nutrients can be related to the thermocline depth, as outlined above, it should be profitable to examine the relationship between the thermocline topography and the distribution of plankton.

The thermocline topography is deduced from bathythermograph (BT) observations taken by naval ships and research vessels of different countries and institutions since 1944. From these data, filed on cards in the BT Section of the Scripps Institution of the University of California, the depth of the top of the thermocline was obtained. This is defined as the transition point on the temperature-depth trace that divides the water column into an upper mixed (almost isothermal) layer and a lower thermocline layer. In most cases this depth was easily determined, but sometimes its identification was difficult due to a weak temperature gradient or to the presence of two or three "small" thermoclines. Such examples were carefully examined, and a depth chosen which agreed with records from adjacent stations. If more than one observation per degree square was made on the same day, the values obtained were averaged. Final averages of thermocline depth were computed, in collaboration with Mr. Cromwell, for each season for areas of one-degree squares.

Most of the available zooplankton data were obtained in the autumn season. Consequently the corresponding chart of thermocline depth (Fig. 1) is based only upon observations between October and December. The number of days in which one or more BT observations were taken within each degree square is also shown. Contour lines joining points with equal thermocline depths have been drawn at intervals of either 10 m (for depths of 0–50 m) or of 20 m (for greater depths). Areas for which there are insufficient data are indicated by broken contour lines.

The most direct comparison between organic production and nutrient supply

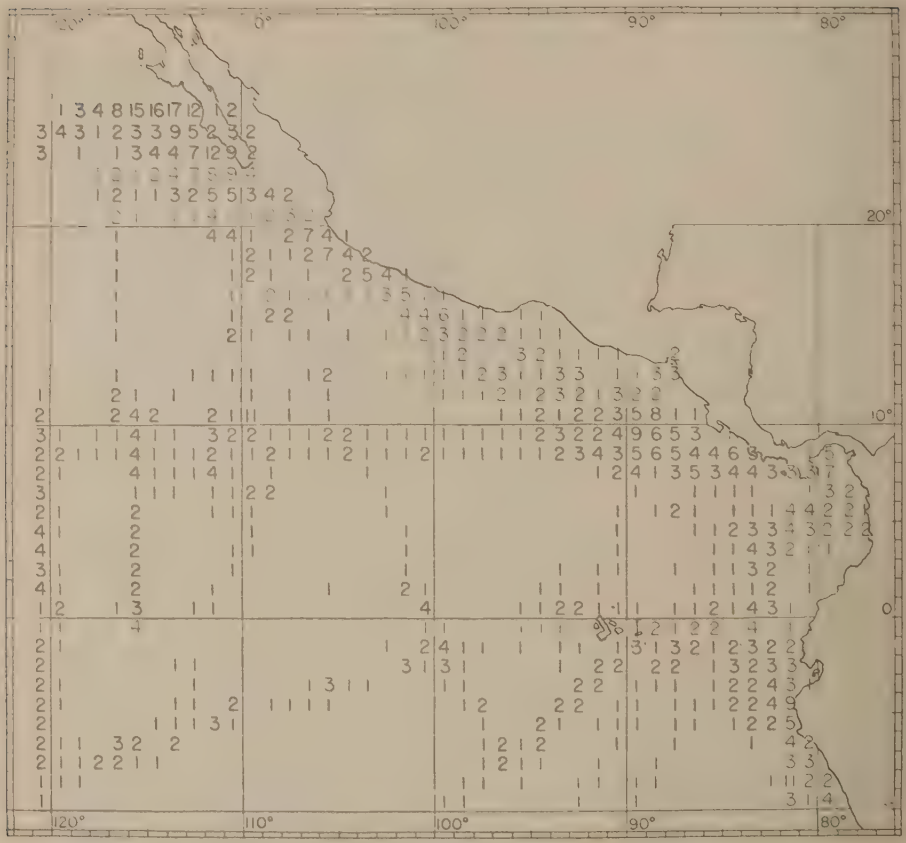

Figure 1 a.

Figure 1 a and b. Mean thermocline depth (m) over the eastern tropical Pacific from bathythermograph observations during October - December in the years 1944 to 1956. The number of observations per degree square is indicated in Figure 1 a.

(as related to thermocline depth) would require measurements *in situ* of photosynthetic production. Only a few such measurements have been made (HOLMES, SCHAEFER, and SHIMADA, 1957; KING, AUSTIN, and DOTY, 1957). In the eastern tropical Pacific, however, there exists a general correlation among production *in situ*, chlorophyll, and zooplankton standing crop as shown by HOLMES, *et al.* (1957, Figs. 12 and 14) and HOLMES (1958). Consequently the zooplankton volume was taken as the index of biological productivity; values were obtained from the routine observations of several expeditions using the oblique net tow. The hauls were made with a one-metre (mouth diameter) plankton net from approximately 300 metres depth up to the surface. Description of the method employed is given in HOLMES, *et al.* (1957, p. 132).

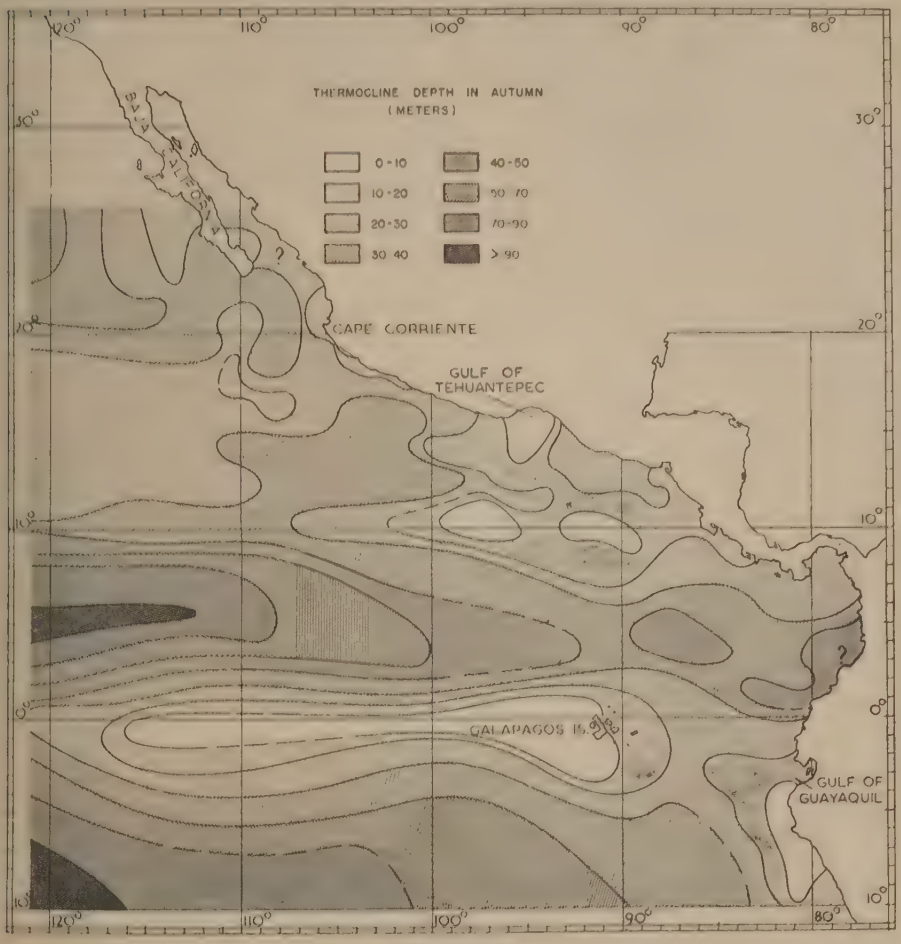

Figure 1 b.

Zooplankton and oceanographical data published in the following reports were used in this study: –

Wooster (1952a); Eastropic Data Report, Scripps Institution of Oceanography (1956); Holmes (1957); King, *et al.* (1957); Wooster and Cromwell, in press; and unpublished plankton data from MLR Cruise 5612, by courtesy of Dr. Elbert H. Ahlstrom, US Fish and Wildlife Service, La Jolla, California.

The zooplankton values (Fig. 2) are given in cubic centimetres of wet plankton (displacement volume) per 1000 cubic metres of water strained, excluding organisms larger than 5 cm^3. The number of observations in each degree square

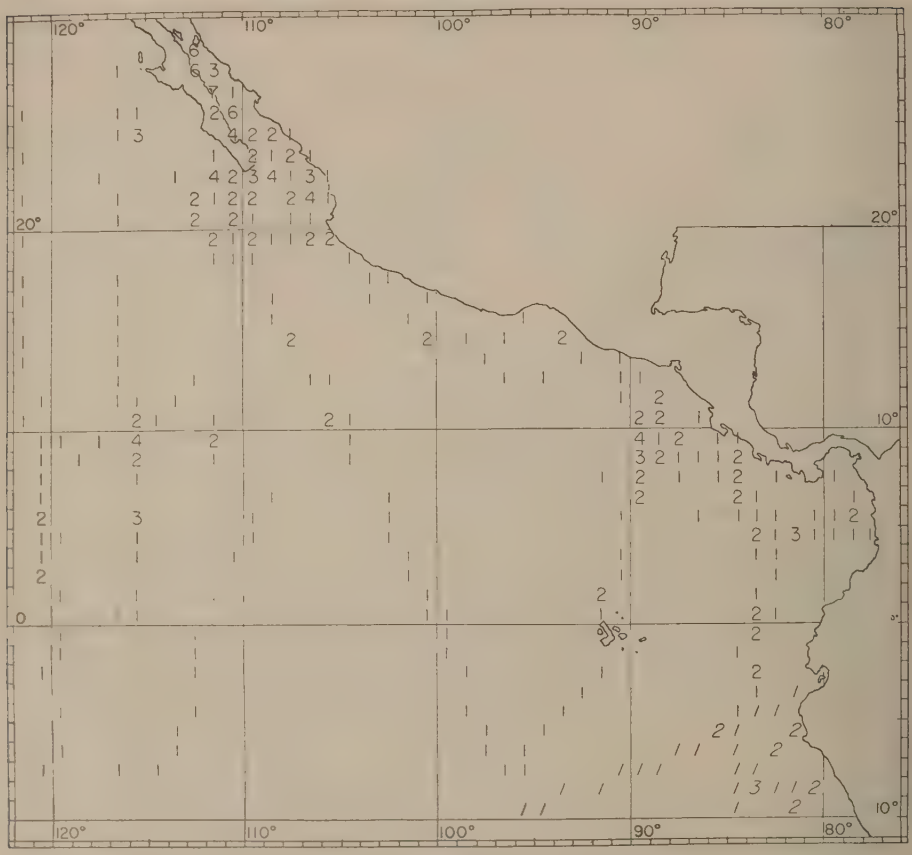

Figure 2 a.

Figure 2 a and b. Mean zooplankton standing crop in wet displacement volume per 1000 cubic m strained, minus the organisms larger than 5 cm³. From observations obtained on "Eastropic", "MLR 5612", and "Scope" Cruises, during October – December in the years 1955 and 1956. In Figure 2 a the number of net tows per degree square is indicated, with earlier summer values from "Shellback" Expedition (1952) given in italics.

is also indicated. Since no net tows have been taken in the area off Peru during autumn, some summer data for this area from the "Shellback" Expedition (WOOSTER, 1952a) are incorporated in the autumn chart (numbers in italics).

The main features of the zooplankton distribution correspond roughly with those of the thermocline topography in Figure 1. An area with a high standing crop of zooplankton is generally also a region with a shallow thermocline depth. Some examples follow: –

(a). In the upwelling zone along the equator between 115° W Long. and the Galapagos Islands, the zooplankton standing crop is between 100 and 200 cc/1000 m³.

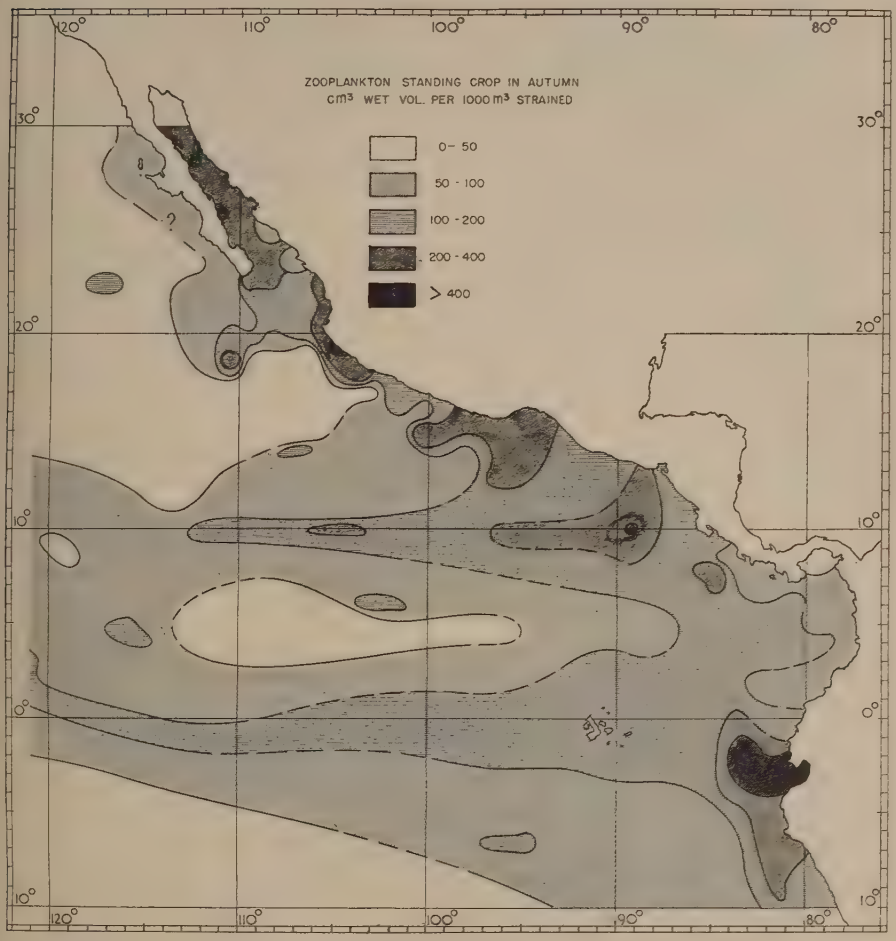

Figure 2 b.

(b). The values for the Central American Ridge, along 10° N Lat., described by WOOSTER and CROMWELL (in press), are as high as those along the equator. In its eastern part, however, they are higher, 200 to 400 cc 1000 m³, and in the region of the shallowest thermocline — the so-called "dome" — more than 400 cc/1000 m³ were sporadically measured.

(c). A very fertile region around the Gulf of Guayaquil, with over 500 cc/1000 m³, is characterized by a shallow thermocline depth of less than 10 m.

(d). The Gulf of Tehuantepec, a shoal area in the thermocline topography, is associated with a high standing crop of 200–400 cc/1000 m³.

(e). Extremely rich plankton catches with more than 500 cc/1000 m³ have been obtained in a small region around Cape Corriente at the Mexican coast, with a thermocline depth less than 10 m.

(f). Values with more than 400 cc/1000 m^3 were found in some inner parts of the Gulf of California. Few BT data were obtained here (see inset chart), and do not allow an interpretation.

(g). An isolated area with a zooplankton standing crop of more than 200 cc/1000 m^3 is located south of Baja California, at about 18°N, where the thermocline is somewhat less than 20 m.

Poor areas correspond in general with a deeper thermocline depth. At the deep trough in thermocline topography along 5°N Lat., associated with the Equatorial Counter Current, low zooplankton values (about 50–100 cc/1000 m^3 or less) were measured. South of the equator there is a region with a standing crop of less than 50 cc/1000 m^3 while the thermocline depth is more than 70 m. On the contrary, a barren offshore area between 12°N and 19°N coincides with a rather shallow thermocline.

Since there are vast areas without biological data, the zooplankton distribution given in Figure 2 cannot be regarded as final. Further collections will be necessary to confirm the apparent relationship.

Fertilizing mechanisms and special hydrographic features associated with high zooplankton standing crop

In addition to indicating the uppermost depth at which nutrients are readily available, the thermocline depth is also related to the prevailing current system, since the mass distribution is rather closely represented by the temperature field.

The moderately high standing crop along the equator is sustained by upwelling. Although this process is well explained for the central part of the Pacific by CROMWELL (1953), it might be useful to illustrate and describe the somewhat different situation in the eastern part by a cross section obtained on the "Eastropic" Expedition (Fig. 3).

In the central Pacific the cool surface water in the upwelling region is imbedded in warm water to the north and south, while the thermocline is situated at about 150–200 m. In the eastern Pacific the South Equatorial Current, which is an offshore extension of the Peru Current, carries cool and phosphate-rich water, and obscures a corresponding strong transition of properties south of the equator. Here the thermocline lies in about 30 m and from this depth the isopleths of thermosteric anomaly [δ_T] (MONTGOMERY and WOOSTER, 1954) from 340 to 500 cl/ton rise sharply, intersecting the surface between the equator and one degree south. One evidence of upwelling, the upsloping of isopleths, is more pronounced in the represented section than in those of CROMWELL (1953, 1954) and AUSTIN (1954) from the central part of the ocean. The phosphate content of the surface in the vicinity of the equator, however, is in both areas similar, ranging from 0·7–1·2 μg-at/l of PO_4-P and indicating favourable conditions for phytoplankton.

The series of sections shown in Figure 3 further demonstrates the conformity between the average condition in the autumn, obtained from several years of BT observations (Fig. 1), and a condition found during two weeks in the autumn of 1955. The thermocline trough at 5°N and the Central American Ridge at 10°N are well pronounced. At the latter, the thermocline might lie above the compensation depth, enabling plant life to exist in the thermocline layer (HOLMES, *et al.*, 1957, Fig. 5.)

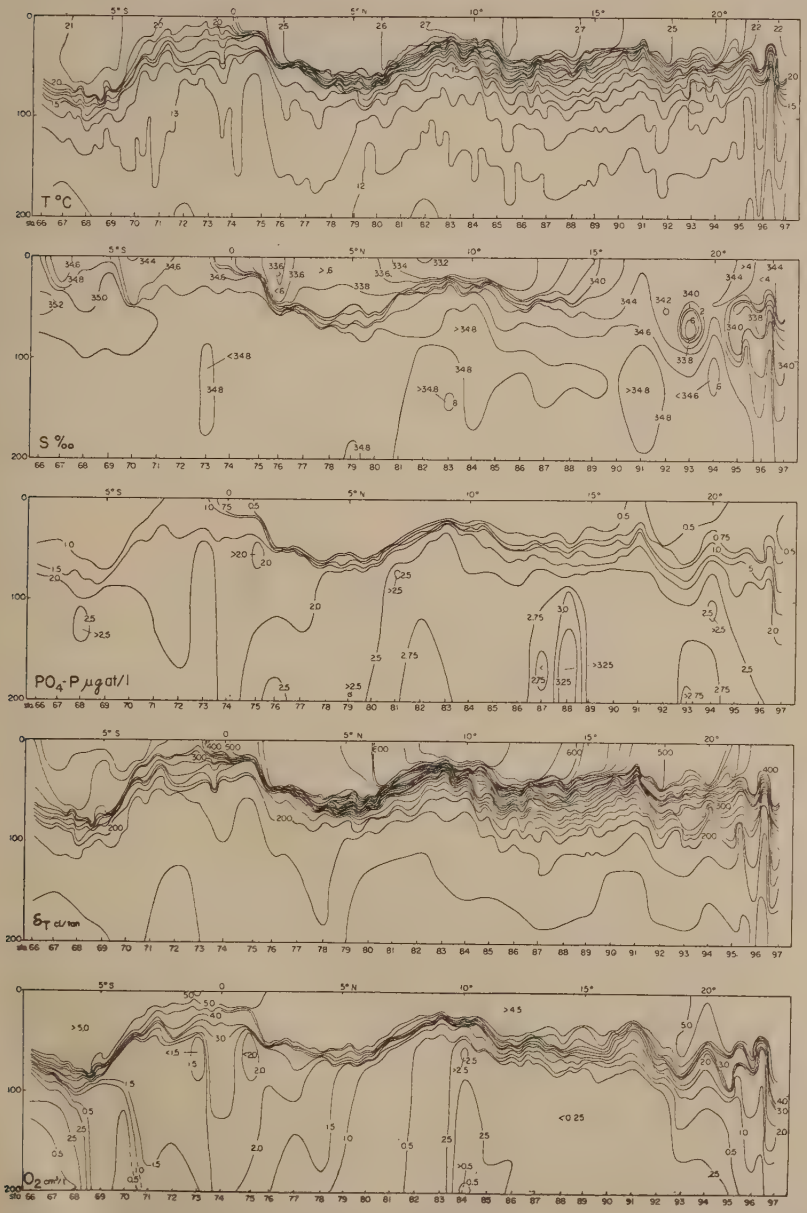

Figure 3. Cross sections showing the distribution of temperature, salinity, inorganic phosphate, thermosteric anomaly, and oxygen during the period 1.–15. December 1955 on "Eastropic" Expedition. Station positions are given in Figure 11.

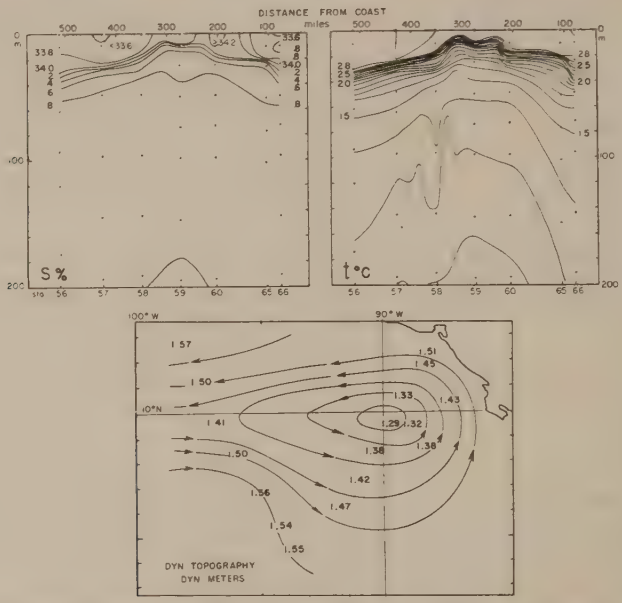

Figure 4a (upper). Cross sections showing the distribution of salinity and temperature during the period 24. May – 4. June 1952 on "Shuttle" Expedition (after WOOSTER and CROMWELL, in press).

Figure 4b (lower). Dynamic topography in dynamic metres over 1000 m during the "Shuttle" Expedition. Station positions are given in Figure 11.

Of further interest is the high surface phosphate at about 17°N (station 91), corresponding with an upsloping of δ_T and salinity isopleths. This feature might be associated with a transition further west (at 124° W) described by WOOSTER and CROMWELL (in press). Net tows carried out on "Eastropic" at this particular station did not yield a high volume of plankton. On other cruises, however, greater catches were obtained in the region at about 17° N, where a shallow thermocline is indicated in the average autumn chart (Fig. 1.)

The "dome", a region of very shallow thermocline off the west coast of Costa Rica was described by WOOSTER and CROMWELL (in press) as associated with the north edge of the Equatorial Counter Current and a northward flowing coastal current inshore. Their "Shellback" and "Shuttle" sections show the thermocline at a depth of about 10 m or less in approximately 9° N Lat. and 89°W Long. In a "Shuttle" section, here reproduced in Figure 4a, salinity values characteristic of the thermocline layer can be found at the surface in the vicinity of this particular feature (station 60). High phosphate concentrations were always encountered here at the surface. The explanation, however, that stirring by wind causes this surface enrichment does not seem to be very satisfactory since the doldrums are centered around this region.

Average charts of surface temperature by SCHOTT (1935, Tables 20–23) indicate cooler water during winter where his current charts (Tables 29 and 30) show a sharp change in the direction of the Counter Current from east

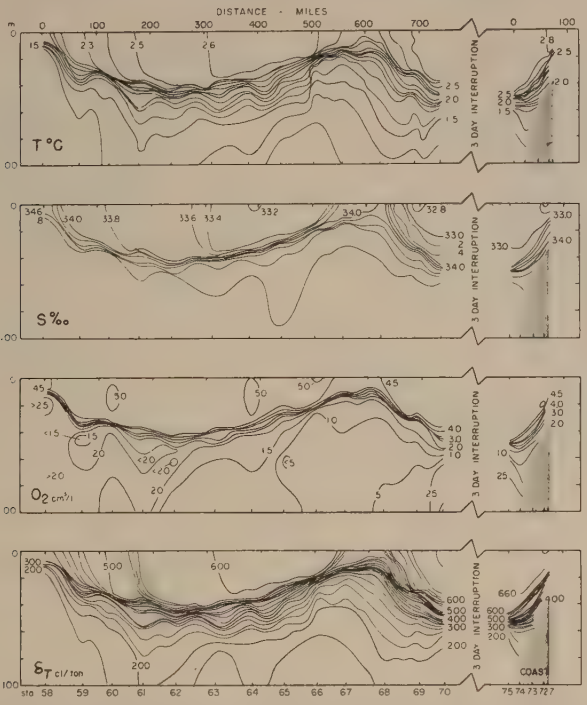

Figure 5. Cross section showing the distribution of temperature, salinity, oxygen, and thermosteric anomaly taken between 28. November and 5. December 1955 on "Eastropic" Expedition. Station positions are given in Figure 11.

toward the north-west, forming partly the westbound North Equatorial Current and partly the northward-flowing coastal current. This suggests an explanation in connexion with the current system.

Changes in the dynamics of this system, e. g., variations in the current velocity of the westbound North Equatorial Current, the eastbound Counter Current or the northbound coastal current require a corresponding alteration of the mass distribution. As the "shear" increases, the slope of the thermocline will also increase with a possible effect of raising the thermocline up to the surface. Such an intersection of the thermocline with the surface, which brings up cool, nutrient-rich water of high salinities, was encountered during the "Eastropic" Expedition.

It can be seen clearly from the sections presented in Figure 5 that the surface layer is very thin and shows properties different from those of the surface layer in adjacent areas. Nutrients become available for plant growth (Fig. 6b), resulting in high zooplankton standing crops of more than 200 (sometimes over 400) cc/1000 m³ (Fig. 2). For demonstration of the flow pattern centered around the "dome", the dynamic topography over 1000 m was computed and drawn both for early summer (May, 1952) and late autumn (Nov.-Dec., 1955) using

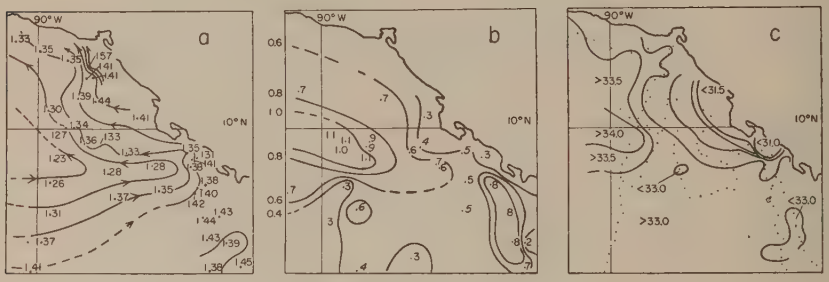

Figure 6. Charts of: –

(a) Dynamic topography in dynamic metres over 1000 m. Stations occupied from 3. November – 7. December 1955 on "Eastropic" Expedition at "dome".

(b) Surface phosphate concentrations, measured in autumn and summer during 1953 to 1956; summer values are in italics.

(c) Surface salinities taken between 3. November – 7. December 1955 on "Eastropic" Expedition.

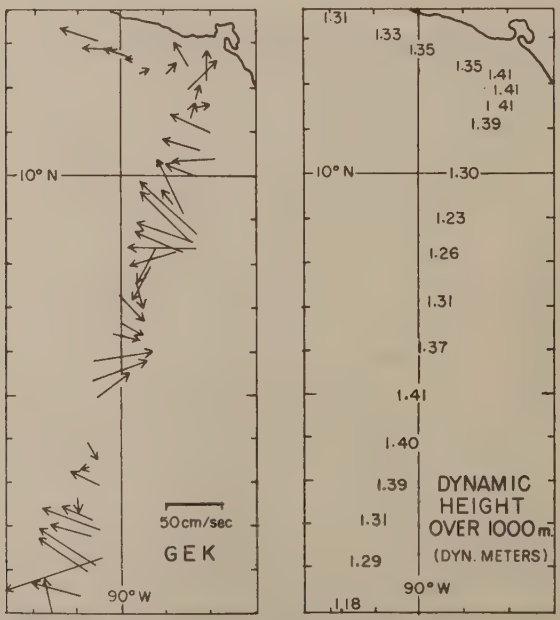

Figure 7. GEK measurements and dynamic height over the Central American Dome. Stations occupied between 28. November and 5. December 1955 on "Eastropic" Expedition (see Figure 11).

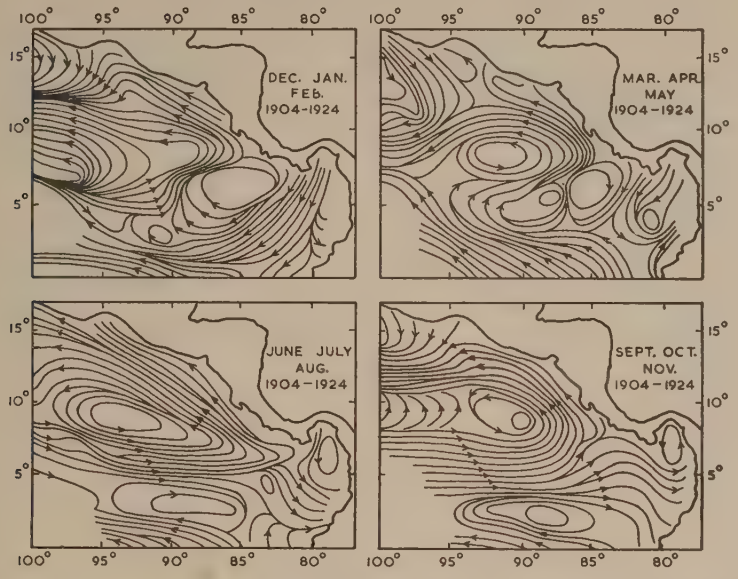

Figure 8. Seasonal variations in the surface currents in the Central American region (after FLEMING, 1940).

data obtained on the "Shuttle" (Fig. 4b) and "Eastropic" Expeditions (Fig. 6a). Both charts show the "dome" present at almost the same location, and Figure 6a reveals that the "dome" can spread out toward the coast of Costa Rica. Unfortunately we have no "Eastropic" data from near this location further west than 90° W, and it is not possible to locate the exact centre. Geomagnetic electrokinetograph (GEK) observations made simultaneously on this profile and the computed dynamic heights do not agree completely as to the position of the "dome" centre (Fig. 7).

A good picture of the seasonal variations of the positions of the "dome" is given by CROMWELL (in press) in his seasonal charts of thermocline topography, and implied by FLEMING (1940) in his streamline charts of the surface current, based on the US Hydrographic Office Pilot Charts (Fig. 8). The δ_T section (Fig. 5) also indicates a south-east-flowing current close inshore along the Costa Rican coast, occupying a shallow depth of less than 100 m. Dynamic heights for these inshore stations were not computed for Figure 6a.

The above mentioned temperature charts of SCHOTT (1935) suggest that "outcropping" might be accentuated during winter in this area, which has an average surface temperature of 2° C less than the surroundings at that season. It is also true that the sections during December (Fig. 5) show "outcropping", those of May (Fig. 4a) merely a higher salinity value at the surface, the temperature difference having been eliminated, probably by solar heating. Two summer sections (WOOSTER and CROMWELL, profiles XIa-d, XVa-h, in press) show only an elevated thermocline. At all three times, however, with or without

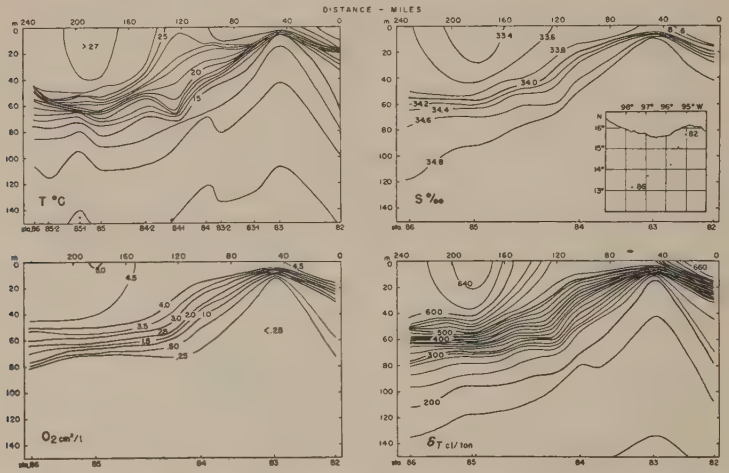

Figure 9. Cross section showing temperature, salinity, oxygen, and thermosteric anomaly in the Gulf of Tehuantepec during the period 9. December to 10. December 1955 on "Eastropic" Expedition. (See Figure 11 for station positions).

"outcropping", high nutrient content at the surface was found, suggesting the possibility of other mechanisms involved in the enrichment process which supports the high production in this area. A study of this phenomenon is being published by CROMWELL (in press).

CROMWELL (1956) suggested that the high standing crop in the Gulf of Tehuantepec is a result of strong mixing by the northerly winds (US Weather Bureau, 1938). These winds are produced by anticyclones to the northward, which blow through the low and narrow Tehuantepec Pass, and sometimes reach gale force in winter. They might cause strong mixing, associated with upwelling.

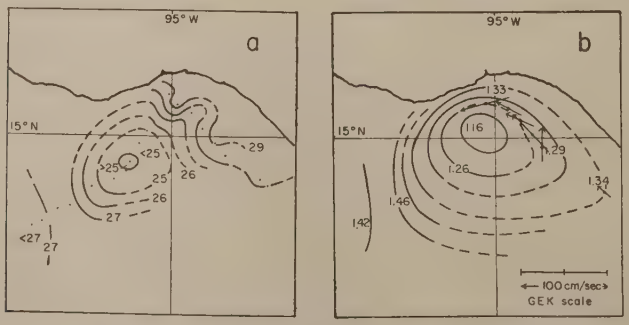

Figure 10. Charts of: – (a) Surface temperature.
(b) Dynamic topography in dynamic metres over 1000 m with few incorporated geomagnetic electrokinetograph measurements. Values obtained during the period 8. December – 11. December 1955 in the Gulf of Tehuantepec on "Eastropic" Expedition.

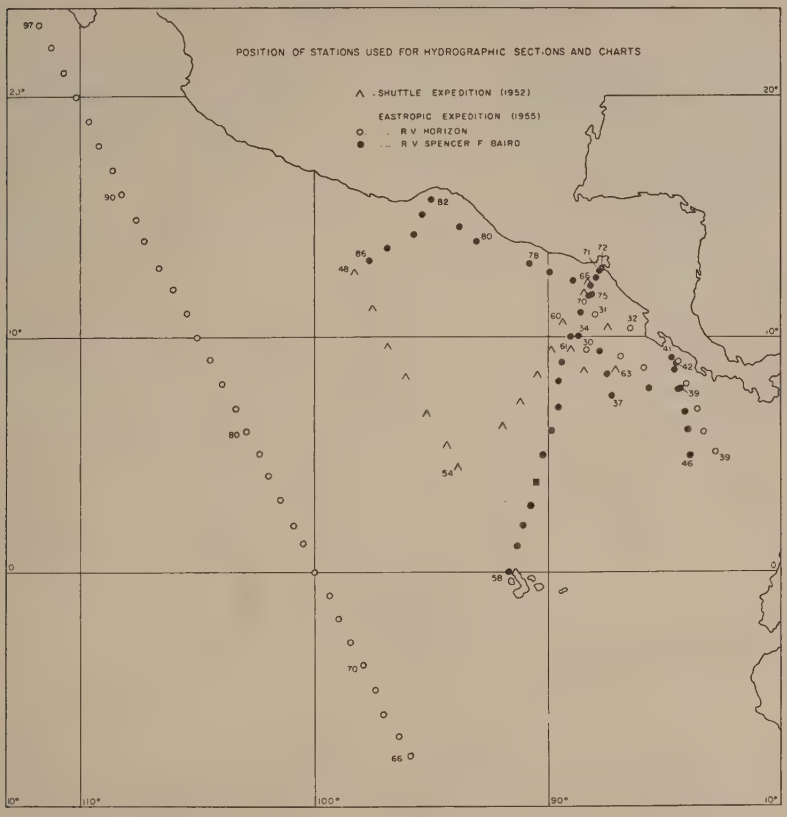

Figure 11. Position of stations used for hydrographic sections and charts.

On the "Eastropic" Expedition a profile through the gulf was completed during strong winds with speeds up to 40 knots. Hydrographic features were found which were very similar to those of the Central American Dome. According to the cross sections presented here (Fig. 9), the centre is located about 70 miles from the coast (station 83). In all sections, here, most isopleths rise very sharply to a depth of 10 m or intersect the surface. Some 150 miles south-west of the centre and 20 miles north-eastward, high oxygen concentrations and temperatures, and lower salinities are found at the surface. The BT station No. 84–1 shows an indication of mixing. Figures 10a and 10b illustrate the surface temperature and the dynamic topography. They incorporate a few GEK measurements which were obtained at the beginning of the storm. From the figures it can be deduced that this "dome" is associated with strong current, circling counter-clockwise in the gulf. It is remarkable that the cool surface water does not coincide with the centre of the dome. This might be due to the strong wind with the possible effect of shifting the cool water southward, but a similar feature is also found over the Central American Dome without stronger winds. SCHOTT's charts (1935, Plates 20 and 24) and the Hydrographic Office

Publications Nos. 570 and 577 also indicate cooler water in this region during the winter.

The fertile region around the Gulf of Guayaquil, by the coasts of north Peru and Ecuador, corresponds to an area with a strong transition between warm equatorial water and the cool upwelling water of the Peru Current. This area is described by several investigators, including SCHOTT (1931); GUNTHER (1936); SCHWEIGGER (1943, 1949); WOOSTER (1952a, 1952b); and WOOSTER and CROMWELL (in press).

The productive regions along the Mexican coast around Cape Corriente, and the inner parts of the Gulf of California, cannot be explained since no BT data are available for the season involved.

Tuna abundance

The results of catch statistics (SHIMADA, 1958; GRIFFITHS, unpublished manuscript) indicate the geographical distribution of the yellowfin tuna abundance, measured both by total landings and by catch-per-standardized-day's fishing. Some of the main areas of high zooplankton standing crop appear as regions of good fishing (e.g., the Central American and Tehuantepec "domes", Gulf of Guyaquil, Galapagos Islands), at least during part of the year. There are too few data to link seasonal fluctuation of zooplankton with those of tuna abundance.

Acknowledgment

I am indebted to Drs. J. F. TALLING, M. B. SCHAEFER, and Mr. Townsend CROMWELL for helpful criticisms of the manuscript.

Summary

1. One of the most important factors influencing aggregation of pelagic fish in tropical waters is the food supply, based ultimately on the production of phytoplankton. Since there is a strong thermocline throughout the year and no seasonal turnover of the water column in large areas of the tropics, the availability of nutrients to the plants is dependent largely upon the depth of the thermocline.

2. A chart of the thermocline topography during the autumn, based on bathythermograph observations, is compared with a chart showing zooplankton distribution. There is an inverse relationship between the depth of the thermocline and the size of the standing crop of zooplankton, which also appears to be related, at least in some regions, to the abundance of tuna.

3. Additional fertilizing mechanisms in certain areas of high standing crop are described by means of cross sections and charts which show dynamic topography and the surface distribution of temperature, salinity, and phosphate.

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Underwater Macrovegetation in Shallow Coastal Waters

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I. Introduction

The present work forms part of a combined biological investigation of shallow indentations on the Danish coasts. Its purpose and start has been described in an earlier publication (GRØNTVED, 1957). The investigations have since been continued in Næraa Strand and Dybsø Fjord. Samples of macrovegetation were collected in the spring and late summer of 1957, and the yield estimated on the basis of the material collected. The investigations done in the spring of 1957 included a third locality, Nibe Broad, which, however, had to be given up later on account of disease in the *Zostera* vegetation. The sampler constructed by me (GRØNTVED, 1957) was again employed for the collection and has given entire satisfaction.

II. Material and Methods

In the laboratory the vegetation samples were rinsed as carefully as possible under the tap; the material was then air-dried, pulverized, and finally dried to constant weight at 110° C. Unfortunately, it is not possible to wash the material absolutely clean by this method; some sand, clay, or mud will adhere to the plants, especially to roots and rhizoids. RØRDAM (1917), who has carried out chemical analyses on *Zostera*, sorted off such impurities by shaking the air-dried plants by which means some sand, mussel shells, and Bryozoa dropped off, as did, however, also some dried leaves and pieces of rootstocks. The weight of this latter material was deducted from the sample proper before the dry matter evaluation took place. I did not do this as parts of plants are unavoidably included in the discarded portion; it is, moreover, impossible to sort off all sand and clay by this method, and a smaller or greater part will remain (RØRDAM, 1917) which part may only be determined from the ashes. Particles from the bottom of sand, clay, or mud, and of epiphytic organisms which it has not been possible to rinse from the plants are weighed together with the dry matter. This percentage is fairly high, and to this the calcareous encrustations on the

Characeae must be added. As it is, moreover, evident that the quantity of impurities is smaller in the *Ruppia* dry matter than in the samples of *Zostera* and Characeae, analyses on nitrogen[1]) have been made so as to have further basis for a comparison between the quantitatively predominating growths.

On each locality it has been the aim to have the stations where the samples are collected evenly spaced over the area, and the samples do in this way each represent approximately equal proportions of the water area of the locality, but a much larger absolute area in Dybsø Fjord than in the smaller Næraa Strand. During the period of investigation the stations were not marked on the spot by poles but only determined by sighting to fixed points on land. On the charts (Figures 1 and 2) they do therefore appear as relatively large circles within which the samples have been collected. In an area where the pattern of vegetation is varied it is thus possible to find different species predominating in the different samplings.

[1]) The determinations of nitrogen, comprising 29 single analyses, have been made by Dansk Mejerilaboratorium A/S, København.

III. Results

The standing crop in Næraa Strand

Næraa Strand (Fig. 1) has a water area of about 430 hectares and a maximum water depth of a little more than 1 m. In the eastern, more shallow part, *Ruppia* (the collective species *R. maritima* L.) forms large unbroken growths on the sand bottom. It also occurs in small patches in the western part. In the middle of the fjord where the depth is greater and the bottom is covered with mud, *Zostera marina* predominates though it does not occur in dense crops, in fact this species is scattered all over the fjord. In the mouth of the fjord where the bottom is sand, the composition of species varies. Here, *Zostera*, *Ruppia*, and *Fucus vesiculosus* occur in small patches with barren areas in between. Masses of *Chaetomorpha linum* are found all over the fjord, drifting with the current, occasionally kept back by the rooted vegetation, or washed up on the beach. Contrary to other higher algae, of which a series of species are represented, this species is quantitatively important in certain samples.

The average values for dry matter were 160, 201, and 361 g/m², respectively on the three days when samples were collected. As regards *Zostera*, strong gales during the summmer and autumn of 1956 had caused a great loss of leaves before the end of October and the value for dry matter is small (210 g/m²).

Table 1

Average values for the standing crop in Næraa Strand

	Entire area		*Zostera* region				*Ruppia* region				The remaining part of the fjord	
	Number of samples	Dry matter g/m²	Number of samples	Dry matter g/m²	% N	Albumen g/m²	Number of samples	Dry matter g/m²	% N	Albumen g/m²	Number of samples	Dry matter g/m²
31. Oct. 1956	28	160	12	210	1·33	17·45	13	122	1·77	13·49	3	126
15. May 1957	28	201	9	346	1·42	30·72	12	94	2·42	14·22	7	198
14. Sept. 1957	28	361	11	487	1·11	33·80	10	234	1·70	24·87	7	346

Figure 1. Næraa Strand on the north coast of Funen. At the stations marked samples have been collected on 31. October 1956, 15. May 1957, and 14. September 1957.

The uncommonly mild winter of 1956–57 undoubtedly benefited the growths so that on 15. May 1957 we found a considerably greater quantity of dry matter than at the previous sampling. It may be assumed that the probable maximum for that year's crop is attained by the middle of September when the dry matter was found to be 487 g/m^2.

Zostera has green leaves the whole year round and its growth is more dependent on weather conditions in the cold season than is that of *Ruppia*, which normally looses the green leaves during the autumn or the winter. By the end of October 1956 this species had shed some leaves. The average dry matter was 122 g/m^2. By the middle of May in the following year new leaves were shooting up, but the preponderant part of the sample material is supplied by the subterranean organs of the species and the value of dry matter was on an average 94 g/m^2. In September *Ruppia* formed vigorous growths, giving on an average 234 g/m^2.

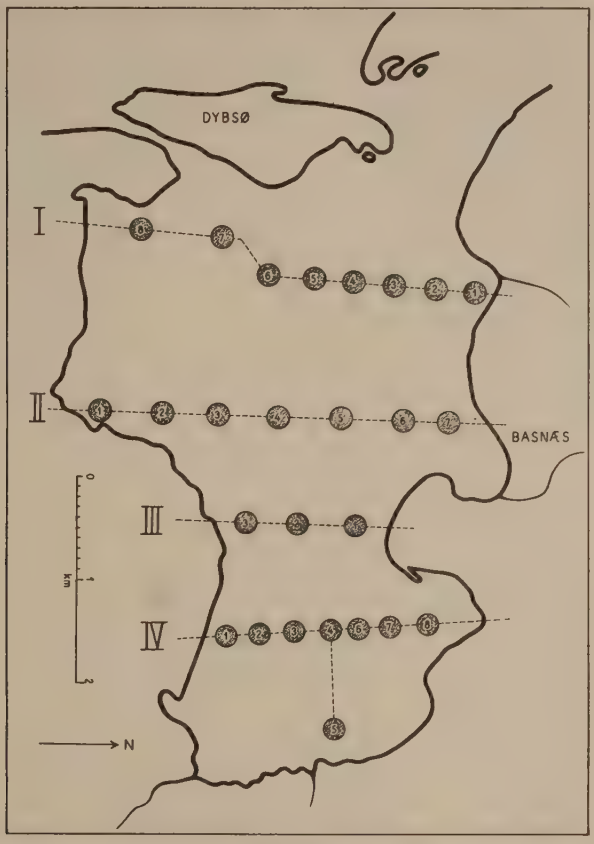

Figure 2. Dybsø Fjord on the south-west coast of Seeland. At the stations marked samples have been collected on 8. November 1956, 9. May 1957, and 7. September 1957.

A comparison between the dry matter in the *Zostera* and the *Ruppia* growths therefore turns out to the advantage of the former species, which in the period of investigation produced on an average about double the quantity of dry matter per area unit than did *Ruppia*.

The remaining samples consisted of mixtures of two or more of the species *Zostera*, *Ruppia*, *Potamogeton pectinatus*, *Chaetomorpha linum*, and *Fucus vesiculosus*. The dry matter content for this group is a little below the average for the whole area of the fjord.

The quantity of albumen, just as is the dry matter, is greater in the *Zostera* than in the *Ruppia* crops, but it is not twice as great. The percentage of nitrogen is relatively high in the *Ruppia* dry matter, which is in part due to the fact that the *Ruppia* samples may, contrary to the *Zostera* samples, be practically free of intermixed bottom material and of epiphytic elements.

Table 2

Average values for the standing crop in Dybsø Fjord

	Entire area		Characeae region				The remaining part of the fjord	
	Number of samples	Dry matter g/m²	Number of samples	Dry matter g/m²	% N	Albumen g/m²	Number of samples	Dry matter g/m²
8. Nov. 1956	26	328	14	436	1·65	44·95	12	203
9. May 1957	26	313	14	389	1·85	44·97	12	224
7. Sept. 1957	26	497	14	672	1·51	63·44	12	292

The standing crop in Dybsø Fjord

The area of Dybsø Fjord (Fig. 2) amounts to about 1700 hectares and has a maximum depth of about 2 m. In respect of vegetation it is possible to divide the fjord into an inner, more shallow part with muddy bottom practically covered by Characeae growths, and a more sandy outer part where these species occur more or less sparsely but where, on the other hand, there are patches of *Zostera*, *Ruppia*, *Potamogeton pectinatus*, and *Fucus vesiculosus*. The samples from this part are often mixtures of two or more of these species. *Chaetomorpha* is found all over the area as are also many other species of higher algae which are, however, of no importance quantitatively in the samples. A survey of the distribution of the species is given by LARSEN (1936).

The Characeae are predominant. The present investigation has given no opportunity for determination of species in the samples but OLSEN (1944), who has dealt with the Danish Characeae at some length with regard to their distribution in Denmark and to their ecological and biological conditions, records the following species from Dybsø Fjord: *Chara aspera*, *Ch. baltica*, *Ch. canescens*, *Ch. horrida*, *Lamprothamnion papulosum*, and *Tolypella nidifica*, but he does not specify the quantitative proportions. As for the duration of life for these species the information from the literature is scarce and in part uncertain. OLSEN (1944) divides the Danish Characeae in two principal groups, annual and perennial, most species belonging to the latter group, and the majority of those normally winter in green state. In shallow waters where the plants are exposed to frost during the winter and where the wash of the waves is strong they tend to become annual. Incidentally, the perennial species do not appear to have a long life in Dybsø Fjord. It can be seen from Table 2 that during our investigations in the unbroken Characeae growths, the maximum value for dry matter was 672 g/m². From this the yearly increment is 672 − 389 = 283 g/m². From the proportion between the maximum crop and the yearly yield it may be inferred that the average lifetime of the Characeae in Dybsø Fjord is only a few years.

The first collection took place on 8. October 1956. Strong gales raged during the autumn and large quantities of loose *Chara* plants and leaves were seen, especially in sheltered places in the fjord and on objects which would hold the drifting plants. The Characeae crops seem, particularly during the autumn, to rid themselves of individuals that are not vigorous. The following winter was uncommonly mild and the fjord was probably not ice-covered, at any rate not during one whole day.

When the next collection took place on 9. May 1957, the Characeae growths

looked very strange; the plants were lying along the bottom of the fjord. They had evidently been in this position during the winter and spring and a thin layer of fine mud had settled on them. A local fisherman told me that this is a normal winter phenomenon and it is a well known fact that a few days later in May the plants would rise to a perpendicular position in the water and that this change from winter to summer state was usually effected in the course of a few days. The material which was collected with the bottom sampler was green, though somewhat pale. The value for dry matter per unit area was somewhat smaller than was the case in November (389 and 436 g/m^2 respectively), and this is explained partly by the presumption that the water movements during the winter loosened some plants, partly in loss by respiration, and finally because great flocks of swans stay in the fjord during the winter and no doubt forage on the Characeae. The vegetation in Dybsø Fjord was again investigated on the 7. September 1957. The Characeae then appeared extremely vigorous; the plants did in most places reach the surface of the water and had a strong green colour; no loose parts of *Chara* plants were observed in the fjord. The average amount of the dry matter was 672 g/m^2. The amount of albumen on the three days when the samples were collected was 44·95, 44·97, and 63·44 g/m^2 respectively.

The samples from the outer part of the fjord which were made up of several species gave a value for the dry matter, which was on an average about half as great as that for the Characeae samples.

A comparison between the quantity of dry matter per unit area in Næraa Strand and in Dybsø Fjord turns out to the advantage of the latter area; the reason for this is to be found in the great content of dry matter in the Characeae samples. If the means of the values for dry matter from all three collections are compared it is seen that the figure for the outer part of Dybsø Fjord and that for Næraa Strand as a whole, are about the same (240 and 241 g/m^2 respectively) but they are only about half as great as the figure (499 g/m^2) for the Characeae area in Dybsø Fjord. The mean for the whole area of Dybsø Fjord is 379 g/m^2 whereas the corresponding figure for Næraa Strand, as just mentioned, is 241 g/m^2.

The yield of the macrovegetation

One of the main purposes of the present investigation is to procure information on the macroscopic plant production (in the sense of increment or yield) in the two areas. Tables 1 and 2 give the figures for the dry matter content of the crops at different seasons and on this basis the yield of dry matter per area unit for the period in question will be estimated.

As regards the *Zostera* vegetation in Næraa Strand we reckon that the minimum content of dry matter in the crop is 210 g/m^2, which value was found at the end of October 1956. The maximum crop was found on the 14. September 1957 when the dry matter content was 487 g/m^2. The increment in this period will then be 487 − 210 = 277 g/m^2. Calculated in the same way the yield of albumen is 33·80 − 17·45 = 16·35 g/m^2. The lowest values for the *Ruppia* crop in Næraa Strand was found on the 15. May 1957. Undoubtedly the crop was smaller earlier in the spring, but we have to reckon with the figure available, 94 g/m^2. The yield is then the difference between the crops on 15. May 1957 and on 14. September 1957. This comes to 234 − 94 = 140 g

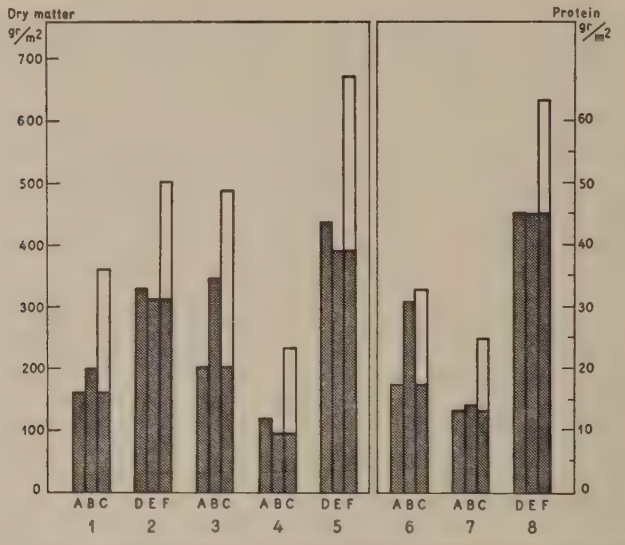

Figure 3. Analyses on the standing crop and calculation of yield of the macrovegetation in Næraa Strand and in Dybsø Fjord. The calculated yield in the period of investigation is shown by a white column.
1. Næraa Strand, the entire area. 2. Dybsø Fjord, the entire area. 3 and 6. Næraa Strand, the *Zostera* samples. 4 and 7. Næraa Strand, the *Ruppia* samples. 5 and 8. Dybsø Fjord, the Characeae region. **A, D** = Autumn 1956; **B, E** = May 1957; **C, F** = August 1957.

dry matter/m², as the yield for the *Ruppia* crops for the summer half-year. The quantity of albumen is 24·87 — 14·22 = 10·65 g/m². In respect of dry matter the increment in the *Zostera* vegetation is then about double the value found in the *Ruppia* area; the ratio in the yields of albumen was on the other hand nearer 3:2. Together these two species cover about three quarters of the area of Næraa Strand; for the remaining vegetation the dry matter yield is 346 — 126 = 220 g/m², that is, a value between those found for *Zostera* and *Ruppia*. The dry matter yield for the total area is 361 — 160 = 201 g/m².

In the Characeae area in Dybsø Fjord we have a minimum crop on the 9. May 1957, with 389 g dry matter/m² and a maximum crop of 672 g/m² in September. The yield of dry matter is here 672 — 389 = 283 g/m², and that of albumen 63·44 — 44·97 = 18·47 g/m². In the outer part of the fjord with the mixed vegetation the dry matter yield is 292 — 203 = 89 g/m². For the whole fjord the yield of dry matter is 497 — 313 = 184 g/m².

The figures for the particular vegetations may be summarized as follows: —

	Yield in g/m²	
	Dry matter	Albumen
Zostera	277	16·35
Ruppia	140	10·65
Characeae	283	18·47

There is no great difference between the yield of the *Zostera* and Characeae vegetations, whereas *Ruppia* has lower values. It may be noted that although the

Characeae always has by far the more dry matter than the *Zostera* crops, the figures for the yield are about the same. This is due to the fact that the Characeae individuals have a longer lifetime than the assimilating organs in *Zostera*.

The dry matter yield during the period of investigation on the two localities is 201 g/m² for Næraa Strand and 184 g/m² for Dybsø Fjord, while the mean value for the dry matter in the standing crops is 241 g/m² and 379 g/m² respectively. The result of this quantitative investigation is then that the macrovegetation in Næraa Strand gives a somewhat higher yield than does that in Dybsø Fjord whereas the standing crop is at any time by far greater in Dybsø Fjord.

It is difficult to assess the importance of the standing crop and the yearly yield from the point of view of fisheries biology and such an evaluation is outside the scope of this work. But PETERSEN (1891) mentions that the invertebrate fauna in the *Zostera* region in Holbæk Fjord is more vigorous than that in the belt along the coast, and in respect of the fish states "that it would probably be right to say that practically all fish in Holbæk Fjord either live permanently in the *Zostera* region or stray into the region to feed". Later (PETERSEN, 1918) he emphasizes that the investigations of the animal population in the *Zostera* region presents great difficulties and is not yet far advanced. This is no doubt also true of zoological investigations in other underwater plant growths.

There is no doubt that the macrovegetation in our fjords, be it *Zostera* or other species, by reducing the water movements, and by serving as a habitat or substratum for animals which fish feed on, and for algae, is of great importance for the fish stock in these places, an importance which may be considered directly proportional to the mass of vegetation.

The standing crop in Nibe Broad

Nibe Broad is an indentation on the eastern, narrow part of the Limfjord, with which it is connected by a broad mouth region; it has some supply of fresh water from the Sebbersund and Halkjær Broads located within. The water area is about 1470 hectares; the depth is in most places quite small and rarely exceeds 1 m.

Samples were taken in the macrovegetation on the 22. May 1957. Altogether 19 samples were taken at places evenly spaced over the area. A nearly unbroken *Zostera* growth forms a wide border in the western part of the broad; in the 8 samples from this region *Zostera* predominates; in the remaining part of the area the vegetation was sparse (with *Codium fragile* and *Fucus vesiculosus* as the quantitatively predominating species). In 6 out of the 11 samples taken outside the *Zostera* border no plant material was found.

Examination of the samples gave the following result: —

	Average dry matter
In all 19 samples	111 g/m²
In 8 *Zostera* samples.....	224 g/m²
In the remaining 11 samples	28 g/m²

In the beginning of July 1957 I again visited Nibe Broad and found that the *Zostera* vegetation in the outer part was not looking normal. Many leaves had turned black in a more or less broad zone round the middle of the leaf or nearer the base. They were liable to break off in this zone and severed parts of

leaves floated in great numbers in the water. The disease resembles the epidemic eel-grass disease which first appeared in our waters in 1933. The sick leaves evidently afford a suitable substratum for the red alga *Melobesia*, because when I visited Nibe Broad again in the middle of August, the eel-grass vegetation in the outer broad was pink practically all over as a result of a dense growth of this alga. In the innermost part of the broad and in Sebbersund Broad, located within, the eel-grass looked normal.

On account of this *Zostera* failure, no samples were taken in Nibe Broad in the autumn of 1957. For comparison with the crops on the other two localities we have only the analyses from May 1957. It gave as stated, 111 g dry matter/m^2 whereas the corresponding figures for Dybsø Fjord and Næraa Strand are 313 and 201 g/m^2 respectively.

IV. Former Danish Investigations on Zostera marina

Since 1933, when the epidemic eel-grass disease first appeared in our waters, the area covered with eel-grass has been reduced to a fraction of its original size (LUND, 1941), and most of the growths now found are not as vigorous as before. Thus to-day the former investigations cannot be said to be of interest quantitatively, yet, they will be considered here.

OSTENFELD (1908) carried out several investigations on the growth of eel-grass. He has, for example, made throughout a year, monthly measurements of the length of all leaves on a number (1–9) of individuals (OSTENFELD's Tables I–IV) and ascertained "that the outermost, i.e., the oldest leaf, is the longest throughout the autumn and winter, whereas in midsummer the second, the third, fourth or even the fifth outermost leaf is the longest". This relative position of the longest leaf throughout the year is important, permitting the conclusion that in the height of summer the leaves will remain, even though their growth is finished or is relatively slow.

On the basis of OSTENFELD's data I have calculated the total length of all leaves on each individual investigated. The result is presented in Figure 4. The plant material originates from two different localities, and they have the common trait that the curve drops in the autumn and early part of the winter, oscillates round an average value in the late winter and the spring and rises to a maximum value in the height of the summer. The values for total length of leaves are greatest in the station with deep water and a muddy bottom and here is also found the greatest difference between maximum and minimum stock.

On the basis of a great number of samples PETERSEN (1913) estimated the production of *Zostera marina* in Danish waters during the summer in the beginning of the century to be 1920, 1120, and 544 g dry matter/m^2 on favourable, medium, and poor localities respectively. The production was estimated by doubling the value of the maximum crop in late summer. PETERSEN calculates the yield valid for the annual yield disregarding the winter yield so as "to correct a possibly too high calculation".

Our calculation of the yield differs from PETERSEN's in that we subtract the plant mass of the spring stock from that of the autumnal stock in order to get the yield of the summer half-year, and no correcting factor is applied for the leaf fall in the summer half-year. In my opinion such a factor would be only a little greater than unity as most of the summer leaves of *Zostera* are shed after the time when the maximum stock in late summer is sampled (cf. OSTENFELD, 1908).

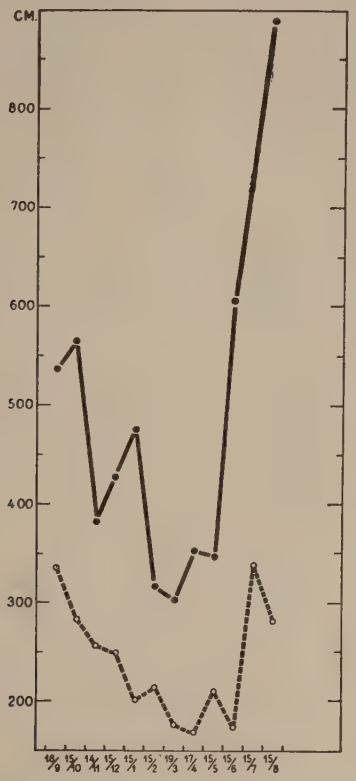

Figure 4. Length of all leaves per individual of *Zostera marina* during one year (1901–02) at localities in the Great Belt near Nyborg.
——— = muddy bottom, depth of water 5–7 m.
– – – – = sand bottom, depth of water 0·5–3·0 m.
(The figures are taken from Ostenfeld's (1908) Tables III and IV, p. 10).

V. Summary

1. Investigations on the macrovegetation have been carried out in two shallow Danish localities, Næraa Strand and Dybsø Fjord, with the aim of estimating the amount of dry matter per unit area during the periods of minimum and maximum growth. The yields are then estimated as the difference between the maximum and the minimum stocks.

2. The dominating species in Næraa Strand are *Zostera marina* and *Ruppia maritima*, whereas in Dybsø Fjord species of *Chara* are quantitatively the most important. In the main, each species covers its part of the fjords and other phanerogams and algae are of smaller or no quantitative importance.

3. Throughout the year the standing crop is greater in Dybsø Fjord than is the case in Næraa Strand, the mean value for the dry matter in the standing crop being 379 g/m^2 and 241 g/m^2 respectively.

4. The annual yields of dry matter in the different vegetation areas are as follows: *Zostera* area, 277 g/m^2; *Ruppia* area, 140 g/m^2; Characeae area, 283 g/m^2. The corresponding yields of albumen are 16·35, 10·65, and 18·47 g/m^2.

5. The total annual yield of dry matter is 201 g/m^2 for Næraa Strand and 184 g/m^2 for Dybsø Fjord.

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The Zoobenthic Biomass in the Southern Baltic

By

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I. Introduction

Although many investigations have been made of the hydrography and biology of the Baltic Sea, there are still not many papers dealing in detail with the quantitative relation between the bottom living organisms and the plankton. Such investigations are of a particular importance as they add to our knowledge of the biological productivity of the sea bottom.

Since the war the Polish Sea Fisheries Institute in Gdynia has carried out very extensive quantitative investigations of the zoobenthos biomass in the southern Baltic. The results were published in the Polish language, and the paper was furnished with only a short summary in English. (DEMEL and MULICKI, 1954). Reviewing the paper, SEGERSTRÅLE (1956) stressed the usefulness of this work, and at the same time expressed regret that the full text of the paper had appeared only in Polish; as a result many biologists interested in the Baltic had not been able to read it. In order to render the paper more accessible to biologists interested in these problems, we are taking advantage of the facilities offered by ICES to publish an English, but nevertheless abbreviated version of the paper.

II. Methods of Investigations

The regions of the southern Baltic covered by the investigations are shown in Figure 1 and includes the area bordered on the north by the latitude of 56°45′ N and on the west by the meridian of 12°30′ E.

Bottom samples were collected with a sampler of standard size; the sampler cut out blocks of 0·1 m^2 from the bottom. As a rule, three samples were taken at each station and this gave in effect a block 0·3 m^2. The rinsing, sieving, and sorting of the material was carried out on board the research ship, and the material from each station was preserved in separate jars in 4% formalin.

Whenever biological material was collected, the depth of water was determined by means of an echo-sounder, the temperature was measured, and water

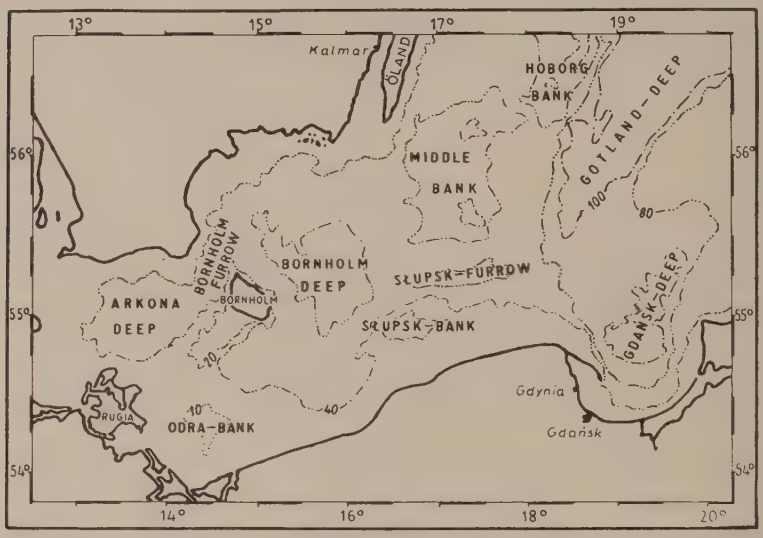

Figure 1. The natural regions of the southern Baltic.

samples collected with a water-bottle for subsequent determination of the salinity and oxygen content. Samples of the bottom sediments were also taken at each station.

The identification of the various species presented no difficulties owing to the small variety present in the Baltic. The invertebrate fauna consists of only a few dozen species.

The difference in the size of specimens were taken into consideration, in order to obtain a more exact estimate of the biomass per unit of surface and of the total biomass. The weight factors were obtained by averaging the weight of a considerable number of specimens of the particular species, for example, 2,500 of the amphipod *Pontoporeia*. The wet weight or, strictly speaking the formalin weight, of the specimens was obtained in this manner and our estimates were based on this weight. The so-called "dry weight" was not used in computing the estimates, although for the sake of comparison the data obtained are calculated together with the wet weight. The "meats" and the shells of mussels were weighed separately, although in our estimates of biomass, only the weight of the meat without the shell was used. The ratio of the weight of meat to shell is given in Table 1.

Table 1

Meat to shell ratios for different molluscs

Macoma baltica	1 : 0·9
Macoma calcarea	1 : 0·5
Astarte borealis	1 : 2·1
Cardium edule	1 : 1·7
Mytilus edulis	1 : 0·6

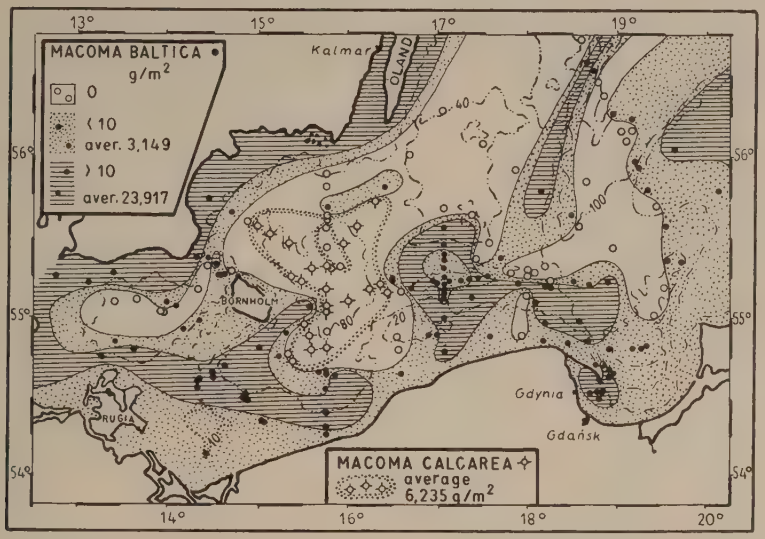

Figure 2. Distribution of *Macoma baltica* (837,000 tons) and *M. calcarea* (47,000 tons) in the southern Baltic.

The estimates made of the biomass per m² were based on a grid of 220 stations, which were close enough to allow "isobenths", that is, lines of equal quantities of zoobenthos per m², to be drawn by interpolation. These in turn served as the basis for the determination of the zoobenthic biomass both for particular species and for all species together.

III. The Biomass of Particular Zoobenthic Species

Mollusca (Figs. 2, 3, and 4)

Macoma baltica L. and *M. calcarea* Chemn. Both species are widely distributed over the Baltic. As compared with its vertical distribution outside the Baltic the distribution of *M. baltica* which in the Baltic covers considerably greater depths to 50–60 m, but it does not occur in the deepest parts (80–100 m) of the southern region. This extension of range in the Baltic is caused rather by an absence of competition in the deep water than by a need for saltier water. It is a predominantly euryhaline species, which can tolerate salinities as low as about 4·0 ‰. In the Baltic the factor which limits the vertical range of this species is the lack of oxygen in the deep water.

M. calcarea occurs in both northern and southern parts of Bornholm Deep. This species can stand the low salinity characteristic of this locality, which is not tolerated by *M. baltica*. The distributions of these two species do not overlap.

The average biomass of *M. baltica* in the shallow waters of the southern Baltic amounts to slightly over 39 g/m²; it is rather more than this on the

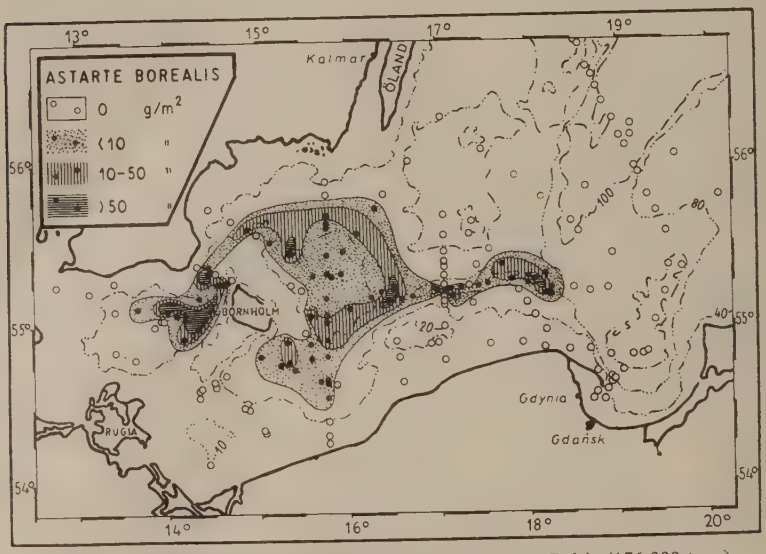

Figure 3. Distribution of *Astarte borealis* in the southern Baltic (176,000 tons).

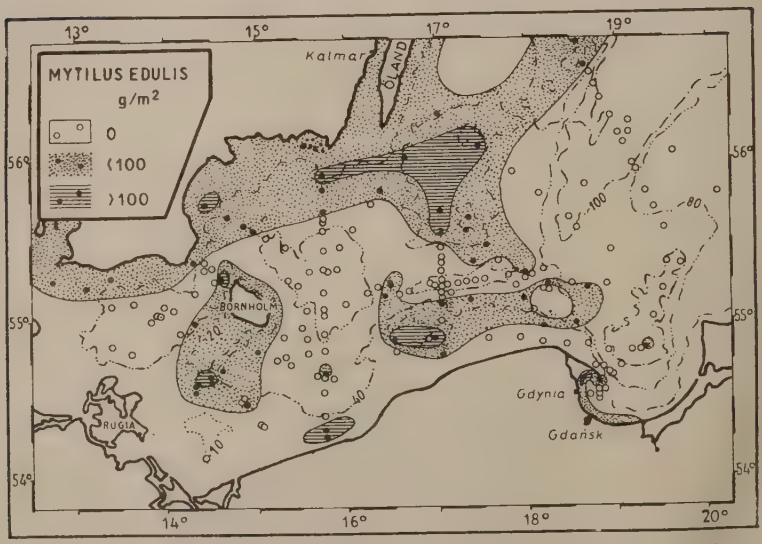

Figure 4. Distribution of *Mytilus edulis* in the southern Baltic (3,400,000 tons).

slopes and reaches a figure of over 24 g/m^2. The total biomass in the southern Baltic is put at 837,000 tons (weight of meat without shell).

The average biomass of *M. calcarea* amounts to 6·23 g/m^2. Its total biomass in Bornholm Basin, the only region in the southern Baltic in which this species occurs, amounts to 47,000 tons.

Astarte borealis Chemn. This mussel occurs in greatest abundance, at over 100 g/m^2 in Arkona Deep and, rather less plentifully in Bornholm Furrow. Areas with lower quantities of 50–100 g/m^2 surround the densest concentrations; these occur at several places in Slupsk Furrow. The lower values are in shallower water. The total biomass of this mussel in the southern Baltic is estimated at 176,000 tons.

Because of its ecological requirements, *Astarte* belongs to the group of mussels inhabiting muddy bottoms and in moving water saturated with oxygen and of high salinity. This accounts for the fact that *Astarte* is found only in the western part of the southern Baltic (Arkona Deep, Bornholm Deep, and Slupsk Furrow).

Mytilus edulis L. This mussel as a rule inhabits a shallow water and is euthermal; it usually spends its life attached to a hard surface. In favourable conditions it produces a biomass exceeding 3 kg/m^2, as at, for instance, off the northern point of Bornholm. In other places the density of *Mytilus edulis* does not reach anything like such values, although it does sometimes exceed 700 g/m^2, as on Middle Bank. Off the southern coast the density in the region of Orla Bank is 163 g/m^2, near Kolobrzeg it is 145 g/m^2, on Slupsk Bank 588 g/m^2, and in Puck Bay 500 g/m^2. There is no *Mytilus edulis* in the clayey bottoms of the Bornholm, Gdansk, and Gothland Deeps. The total biomass in the southern Baltic is very large, 3,400,000 tons.

Crustacea (Figs. 5, 6, and 7)

Mesidotea entomon. This Arctic relict species is found mostly in the northern and western regions of the Baltic. The southern Baltic is the limit of its range, which accounts for its rather patchy distribution in Bornholm Basin and Arkona Deep. It avoids the deepest parts of Bornholm Deep, which is of relatively high salinity and low oxygen content, as well as the shallower sandy bottoms between Ustka and Rozewie and on Slupsk Bank. It does not occur in Gdansk Deep, in spite of the fact that the maximum density found, 28·64 g/m^2, was observed on the slopes of Gdansk Bay. The next greatest density of 17·18 g/m^2, was found off the Hel Peninsula, and third, of 11·45 g/m^2, between the Orla and Odra Banks. The whole biomass of the region investigated amounted to 49,000 tons.

M. entomon belongs to the brackish-freshwater group. It avoids shallow water and sand banks, being a stenothermal cold-water species.

Pontoporeia femorata Kröyer and *P. affinis* Lindström.

From the chart showing the distribution of these amphipods in the southern Baltic, it appears that the differences in range are due to the different ecological requirements of the two otherwise similar species. The two groups occupy the same general areas, that overlap each other only slightly. *P. femorata* is found in relatively deep water and on bottoms of mud and clay; it feeds on this bottom, as it belongs to the ecological group which obtains nourishment from slime. It cannot stand such low salinities as *P. affinis* which reaches as far

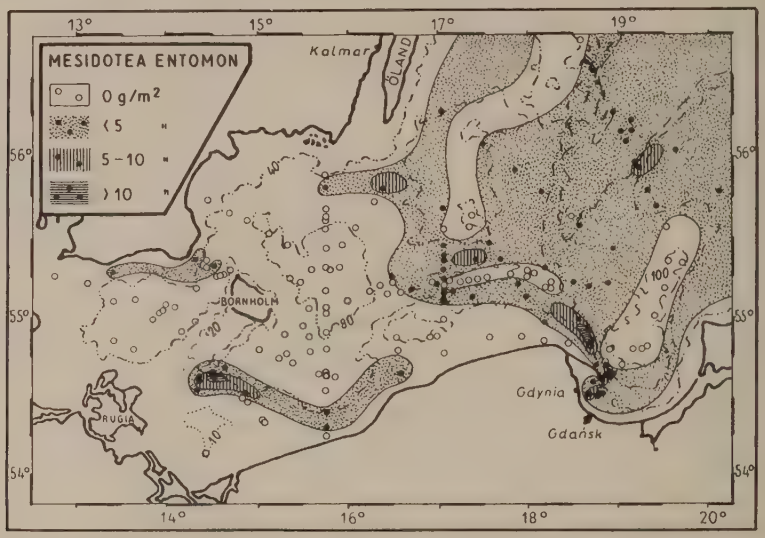

Figure 5. Distribution of *Mesidotea entomon* in the southern Baltic (49,000 tons).

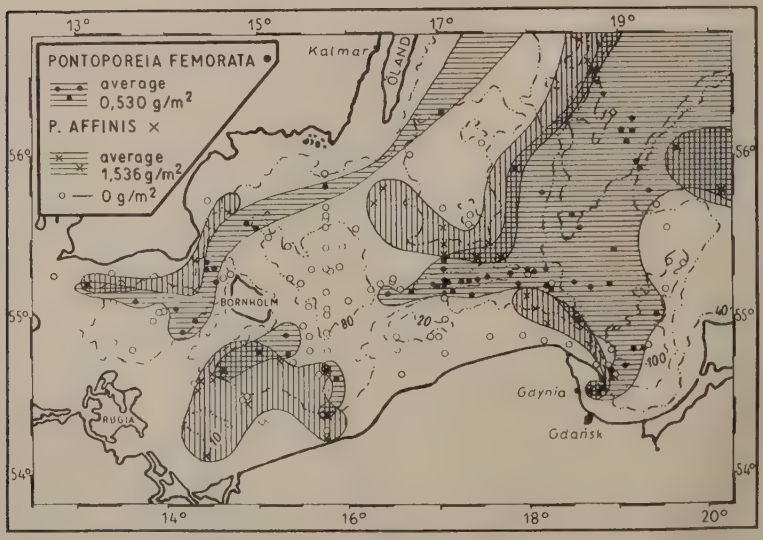

Figure 6. Distribution of *Pontoporeia femorata* (20,000 tons) and *P. affinis* (30,000 tons). in the southern Baltic.

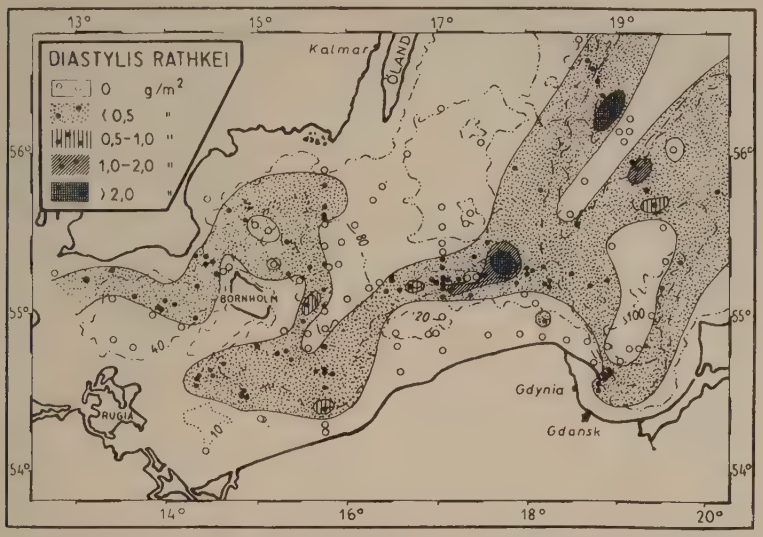

Figure 7. Distribution of *Diastylis rathkei* in the southern Baltic (7,000 tons).

as the northern parts of the Gulf of Bothnia. *P. affinis* occurs mostly on sloping bottom and sometimes in shallow water, but never in the depths in which *P. femorata* is found. In parts of the southern Baltic, in the southern part of the Middle Bank, its biomass amounts to 3·425 g/m²; this corresponds to over 1,000 specimens per 1 m². The average biomass of *P. femorata* in the southern Baltic is 0·530 g/m²; that of *P. affinis* is 1·556 g/m². The total biomass of *P. femorata* is 20,000 tons and that of *P. affinis*, 30,000 tons.

Diastylis rathkei Kröyer. This crustacean is a deep-water species, inhabiting waters deeper than 40 m. It is therefore not to be expected that this species would be found in the southern Baltic in shallow waters less than 40 m deep. Locally the density of *Diastylis* amounts to 1–2 g/m². The maximum density in the southern Baltic was observed in Slupsk Furrow, especially the eastern part. It was also found on the sloping bottoms of the southern part of Gothland Deep. At Station 170, 528 specimens were taken per m². The total biomass in the southern Baltic is 7,000 tons.

Polychaeta (Fig. 8)

Scoloplos armiger O. F. Müller. As this animal swallows the soil in which it lives, it occurs on slimy, and slimy-sandy bottoms in fairly deep water all over the southern Baltic. The biomass varies from 0·03 g/m² in the southern parts of Gothland Deep to 7·52 g/m² in the north-western part of Bornholm Basin. The western part of Arkona Deep and Bornholm Furrow are characteristic by the presence of this specimen in considerable quantities, more than 5 g/m². The biomass of this polychaete over the whole of the southern Baltic amounts to 37,000 tons.

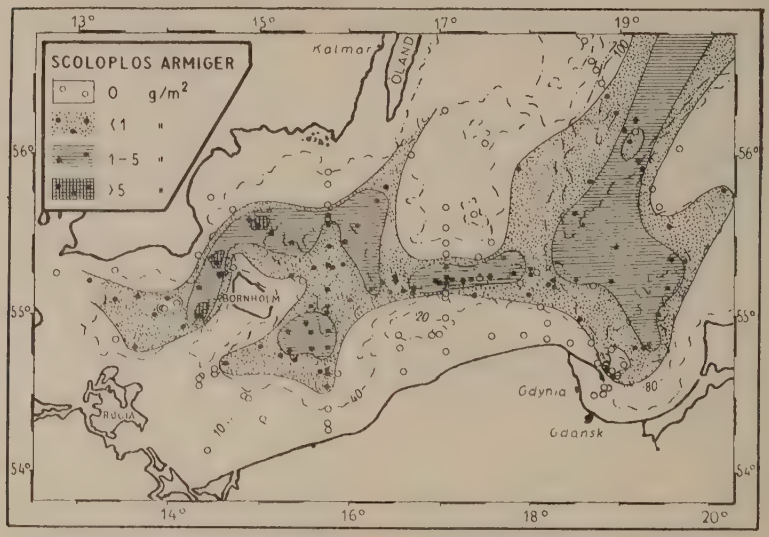

Figure 8. Distribution of *Scoloplos armiger* in the southern Baltic (37,000 tons).

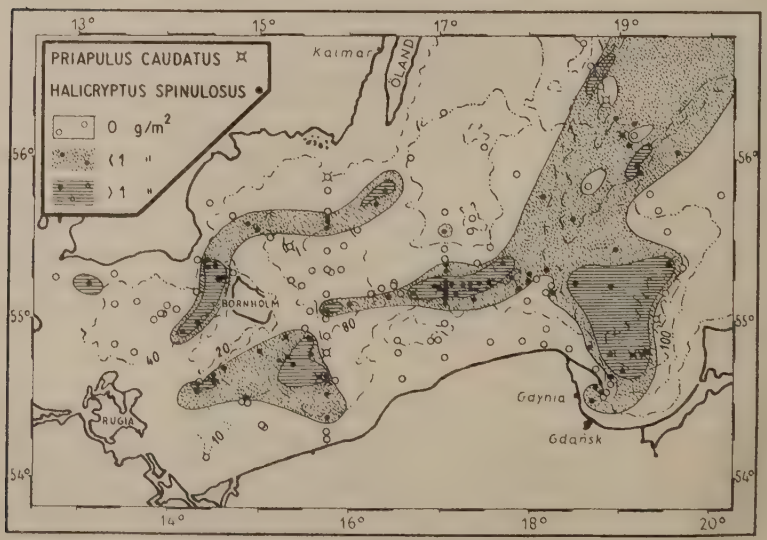

Figure 9. Distribution of *Halicryptus spinulosus* (28,000 tons) and occurrence of *Priapulus caudatus* in the southern Baltic.

Priapulidae (Fig. 9)

Halicryptus spinulosus V. Sieb. The distribution of this species, as illustrated in the chart, clearly shows that ecological requirements are a decisive factor in its distribution. It requires cold and relatively salt water, which accounts for its appearance in deep water. The greatest density of the biomass, 3·89 g/m², was found in Slupsk Furrow. A slightly lower density exceeding 2 g/m², however, was observed in Bornholm Furrow and Gdansk Deep. Our data complement EKMAN's (1933) chart to a considerable extent, and locate this species mostly in the western and south-eastern regions of the Baltic Sea proper. The biomass for the whole southern Baltic amounts to 228,000 tons.

Priapulus caudatus Lamarck occurs, as a rule, in relatively deep, cold water, which suggests that it is stenothermal. The shallowest waters in which it is found are off the south coasts of Sweden in a depth of 18 m. The places in which it occurs are shovn in Figure 9.

IV. The Zoobenthic Biomass in the Southern Baltic as a Whole

The biomass in the whole of southern Baltic, that is the region bordered on the north by latitude 56°45′N and on the west by the meridian of 12°30′E, has been estimated at 1,356,000 tons. This value excludes *Mytilus edulis*, the biomass of which was found to be 3,400,000 tons; thus the total biomass, including *Mytilus edulis*, amounts to 4,756,000 tons. It should be noted that the biomass of the mussels was estimated without the shells which weigh about 1,000,000 tons. The zoobenthic biomass per m² in different parts of the southern Baltic (Fig. 10) varies from 3·48 to 171 g/m² which corresponds to an average of 11·5 g/m², not including *Mytilus edulis*, with *Mytilus*, 40·7 g/m².

V. The Zoobenthic Biomass at Various Depths

We may distinguish the following depth zones in the southern Baltic: shallow water, 0–40 m deep; sloping bottoms from 40 to 80 m, and deep water over 80 m deep.

The total biomass in the shallow waters of Arkona Basin, excluding the local *Mytilus* communities associated with a hard bottom, amounts to 25·61 g/m²; the value on the sloping bottoms is higher, and amounts to 30·53 g/m²; the average biomass over all the Arkona Basin is 28·77 g/m².

The total biomass in Bornholm Basin is less than in Arkona Basin. The average value drops fairly regularly from 19·21 g/m² in the shallow water to 16·77 g/m² on the slopes, and 9·41 g/m² in the deep water.

The heaviest biomass of 31·66 g/m² occurs in Slupsk Furrow. It is slightly less in the deep water, 24·47 g/m², and the lowest value, 14·09 g/m², is associated with shallow water.

In the southern part of the Gothland Basin, which wedges into the southern Baltic, the shallow water is notable for its heavy biomass, 76·38 g/m², while on the slopes it is 66·75 g/m². Conditions in these zones differ very markedly from those in the deep water, in which the biomass is only 4·46 g/m². It should be added that the comparatively high value of the biomass in the shallow water and on the slopes is largely due to the occurrence of mussels, which constitute four-fifths of the biomass per m². Owing to the poor circulation and

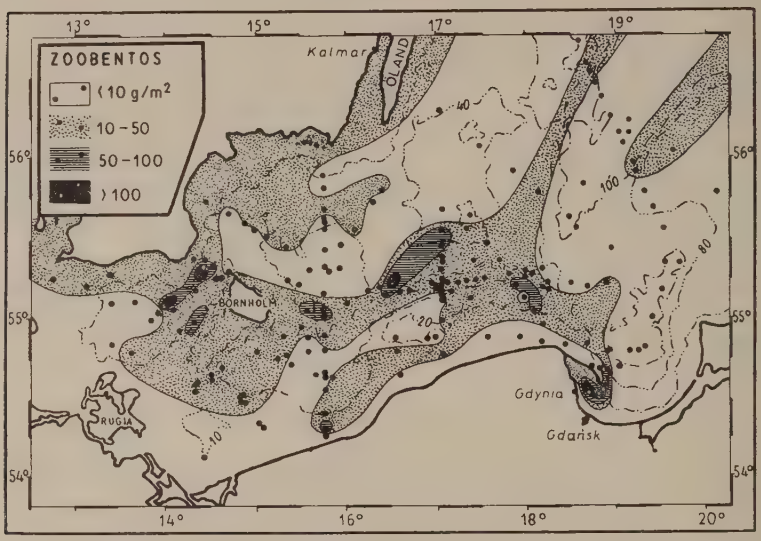

Figure 10. Distribution of zoobenthic biomass, without *Mytilus*, in the southern Baltic.

oxygenation the quantity of mussels markedly decreases towards the deep water; Slupsk Furrow which is well oxygenated, and in which the biomass of *M. baltica* and *Astarte* together constitute 16·90 g/m², is an exception.

VI. The Vertical Distribution of Different Orders

The crustaceans are most numerous on the slopes of Slupsk Furrow and in the Gothland Basin at a depth of 40–80 m. Their biomass was 3·70 g/m² in the Gothland Basin, and 2·51 g/m² in Slupsk Furrow. In the Bornholm and Arkona Basins the largest biomass of crustaceans is found in shallow water less than 40 m deep.

The worms, nemertines, and sipunculids increase in numbers as the depth increases. This is true for Arkona Basin, Slupsk Furrow, and the Gothland Deep. The most dense worm population was found in Slupsk Furrow with a biomass of 6·57 g/m² at stations with depths greater than 80 m.

VII. Practical Aspects of the Problem

Studies of the biological yield of the sea bottom, which can be estimated from measurements of the biomass are clearly of practical significance. They are closely concerned with the problem of the food of commercially valuable fish. Apart from plankton organisms and small fish, the benthos and particularly the zoobenthos is both a primary and a secondary source of food for the fish in the sea. It is directly eaten by demersal and bottom-living fishes. While it is

not always an easy matter to determine the quantities taken by the fish from this source as our knowledge of the feeding habits of fish and the nature of their food is limited, a determination of the biomass is the only means by which we can estimate the approximate yield. Mussels, a biomass of over 4 million tons, appear to be the largest food resources in the southern Baltic. However, they are eaten directly only by flatfish. For other fish they are an indirect source of food.

The other groups in the benthos play a minor part, their biomass amounting to slightly over 300,000 tons. Crustaceans contribute slightly more than 100,000 tons of biomass and in view of the nature of life cycle their annual yield or production is probably similar in amount. They are suitable as food for demersal and bottom living fish, as well as for pelagic species in certain stages of their lives. Further investigations on the feeding of the fish might explain to what extent they require various kinds of food.

VIII. Summary

1. The work on the biological yield of the sea bottom in the southern Baltic is a continuation of the former Polish studies of the bottom fauna in this region. From a close grid of 220 stations estimates were made of the zoobenthic biomass in g/m² and of the total biomass in tons for the whole region.

2. The following biomass values for the various species were found.

Table 2

Species	Mean biomass g/m²	Total biomass for the whole southern Baltic in 1000 tons
Macoma baltica	3·1–23·9	887
Macoma calcarea	6·2	47
Astarte borealis	10–100	176
Mytilus edulis	0·03–3,100	3,400
Pontoporeia affinis	1·5	30
Pontoporeia femorata	0·5	20
Mesidotea entomon	0·7–28·6	49
Diastylis rathkei	0·5–2·0	7
Others		191
Total		4,807
(excluding *Mytilus*)		1,407

3. The zoobenthos of the southern Baltic is most abundant in the vicinity of Bornholm Furrow, in the western part of Slupsk Furrow, and off the Hel Peninsula. The edible mussel, which provides a larger biomass than all the rest of the zoobenthos, occurs in greater numbers in relatively shallow water, where the bottom is hard and stony, or else consists of grained sand, this being an indispensable requirement for this mussel.

4. Sloping bottoms in depths from 40 to 80 m seem to be the most productive. This is true for both western and eastern regions of the southern Baltic. The yield of these regions increases from west to east. The biomass is very low in depths over 80 m. This is most likely associated with the lack of oxygen in the near-bottom waters layers, although these waters are, as a rule, more saline. The yield of shallow waters less than 40 m deep, however, varies widely. Loose,

shifting sands are characterized by their small biomass, while stony bottoms are sometimes inhabited by compact communities of edible mussels, with a biomass exceeding 3 kg/m^2.

5. The largest biomass is that of the mussels, especially *Mytilus*, which rely for food on material present in deep water. *Macoma* is distributed in the littoral and sublittoral regions of the Baltic. The value of its biomass suggests that it constitutes an important food reserve for flounder.

6. The total biomass of the bottom-living crustaceans is a little over 100,000 tons. They are a source of food suitable for herring, cod, and flounder. The low biomass of these crustaceans suggests that the cod feeds on other sources as well, such as the near-bottom fauna, such as *Mysidacea* and fish.

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Description of Model Used to Demonstrate Dynamics of Exploited Fish Stocks

by

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I. Details of Construction

As part of an exhibition of fisheries research at the Lowestoft Fisheries Laboratory, a model which promises to be useful in illustrating the main theory of fishing dynamics, has been designed and constructed by the staff. It shows the participation of the four factors: age at first capture, fishing mortality, natural mortality, and average weight at each age. The first two are within human control, the third and fourth are properties of the population estimated from data. The present model could probably be improved on, but it is quite adequate for its purpose, which is demonstration of the theory in a simple visual form. A photograph of the model is shown in Figure 1 and a line diagram in Figure 2.

The active part of the model consists of a flat piece of $\frac{1}{2}''$ plywood (12 mm) $74'' \times 30''$ on which are mounted five boxes, each measuring $9'' \times 9''$ and having a depth of $\frac{3}{4}''$. Through these boxes are fed the "fish", represented by ball bearings $^3/_8''$ diameter. Each box (A) represents one year of life of the fish, is faced with perspex and is set with $1''$ "panel pins" nailed into the plywood back of the box. The function of these pins, which are arranged in staggered rows $\frac{1}{2}''$ apart, is to scatter any ball bearings dropped into the top of the box, and randomize their distribution before they reach the bottom of the box. On the top of each box the perspex front, and the sides of the box are extended upwards to form a trough (C), the base of which is formed by a metal plate (D) hinged in such a way that it can be turned from the outside of the box to allow any balls in the trough to fall into the box. Each box is placed directly under the one above, so that any balls falling out of the first box are collected in the trough on top of the second, and from there can be released to fall through the subsequent box.

At the bottom of each box two slides are arranged. Each of the metal slides is the width of the box (A) and serves to catch any balls falling into the slide

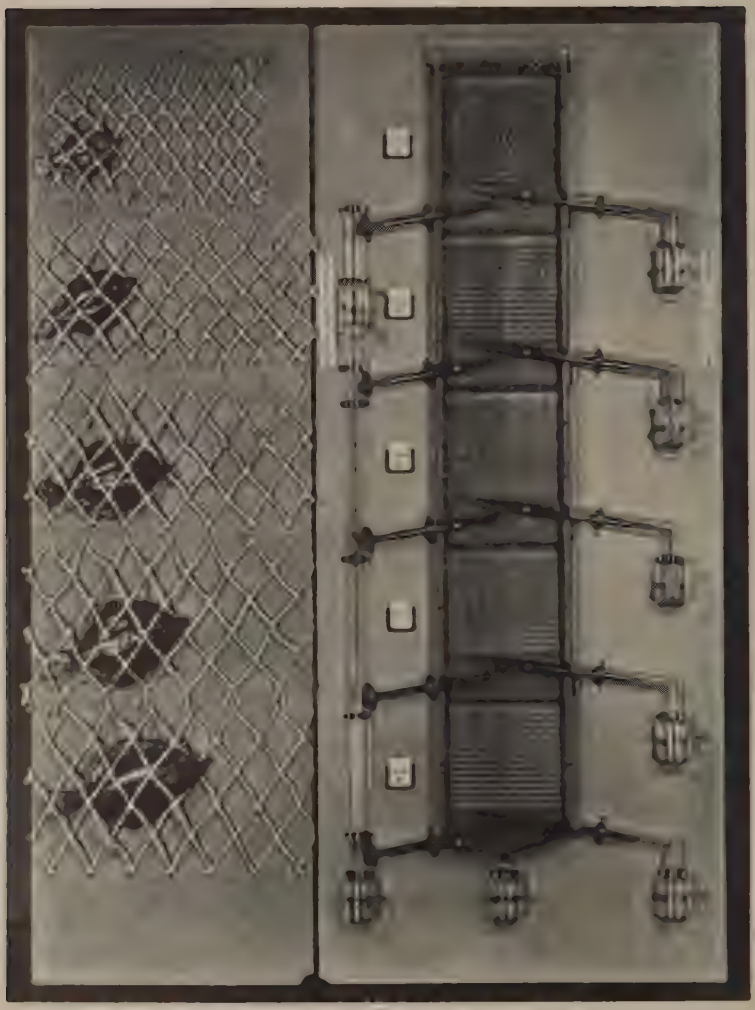

Figure 1. Photograph of model.

and lead them to the tube (J). The slides on the left hand side (E) represent natural mortality and can be moved across the bottom of the box so that they occupy up to $^1/_3$ of the distance across the box. (It was thought that not more than $^1/_3$ of the population would be lost to natural causes in the majority of examples.) If a larger natural mortality is desired, there is no reason why the slides should not be made longer. Attached to the slide is a handle (F) which enables adjustment to be made to obtain the amount of natural mortality

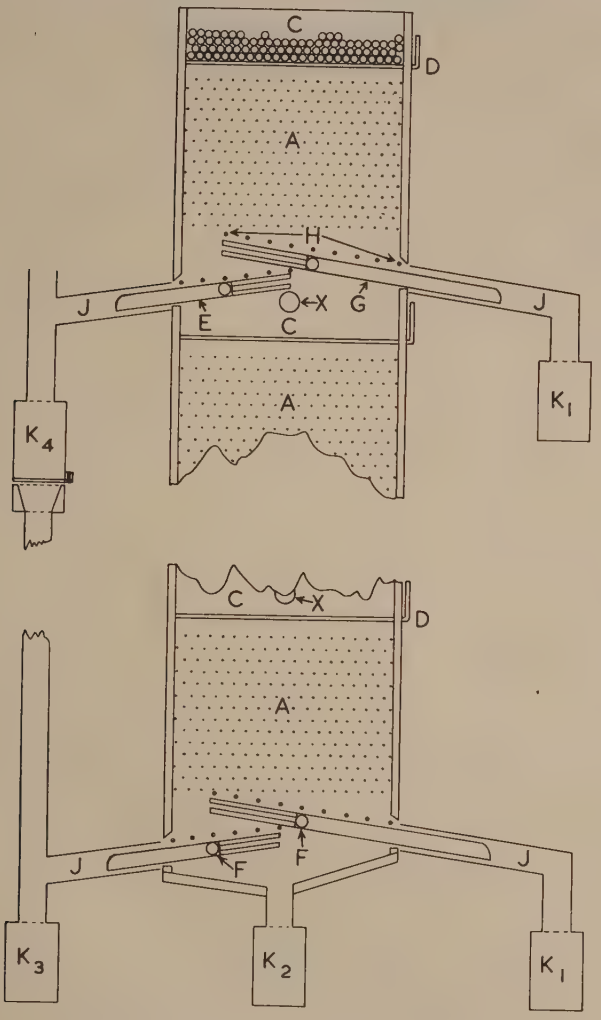

Figure 2. Line drawing showing details of model.

required. On the right hand side of the boxes are other slides (G) which can extend up to $^3/_4$ of the way across the box and represent fishing mortality.

Above each slide is a graduated scale (H) to give the settings of these slides. The slides feed directly into tubes (J) ending in detachable perspex boxes which serve to collect any ball bearings (fish) taken from each box (year). In the case of natural mortality the balls can all be led into one collecting box (K_3) or the natural mortality from the first year can be kept separate by collecting the balls

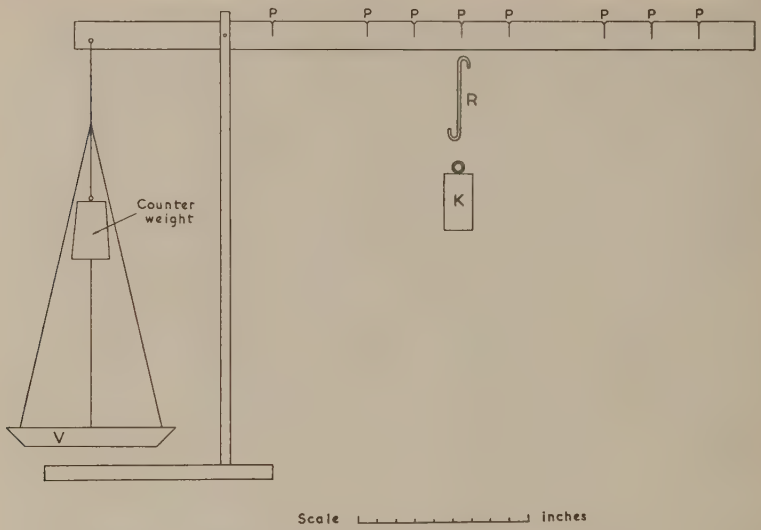

Figure 3. Steelyard used for estimating weight of "fish" taken.

in collecting box (K_4), and all balls extracted from the subsequent years allowed to run into box (K_3).

The balls extracted by fishing mortality from each year are collected in the boxes (K_1). At the bottom of the last box (year 5) any balls which are not removed either by fishing or natural causes drop into a collecting box (K_2) representing the survivals, or, better, the last year box may be called "5 plus" and its base divided wholly by the slides in their appropriate proportions. All fish would then be lost through fishing and natural causes.

All the collecting boxes (K_1, K_2, K_3, and K_4) are the same size and weight, and are labelled to indicate first year natural mortality, first year fishing mortality, etc., and spare boxes are supplied for use when required in some demonstrations.

At the top of each year box (A) except for that of the first year, a hole (X) is made on the perspex front through which balls can be introduced to the trough (C) of each of the later year boxes. These balls represent recruits.

The second part of the model assesses the results. This may have several forms, two of which will be described.

A steelyard, Figure 3, constructed of a piece of steel 3 feet long, is pivoted on a stand. On one end of the steel bar a pan is suspended on which weights may be placed. The steel bar is graduated so that the boxes can be hung up at the correct distance from the fulcrum, the distance being proportional to the average weight of the fish in question at each age. For convenience, notches (P) are made for two of the common species, plaice and herring. For plaice, these are made in the ratio of 1 : 3 : 5 : 8 : 10 units from the fulcrum. Hooks hang in these notches, and the collecting boxes are suspended by them in the appropriate notch. Thus each year of fishable life of a brood makes its contribution to the moment on

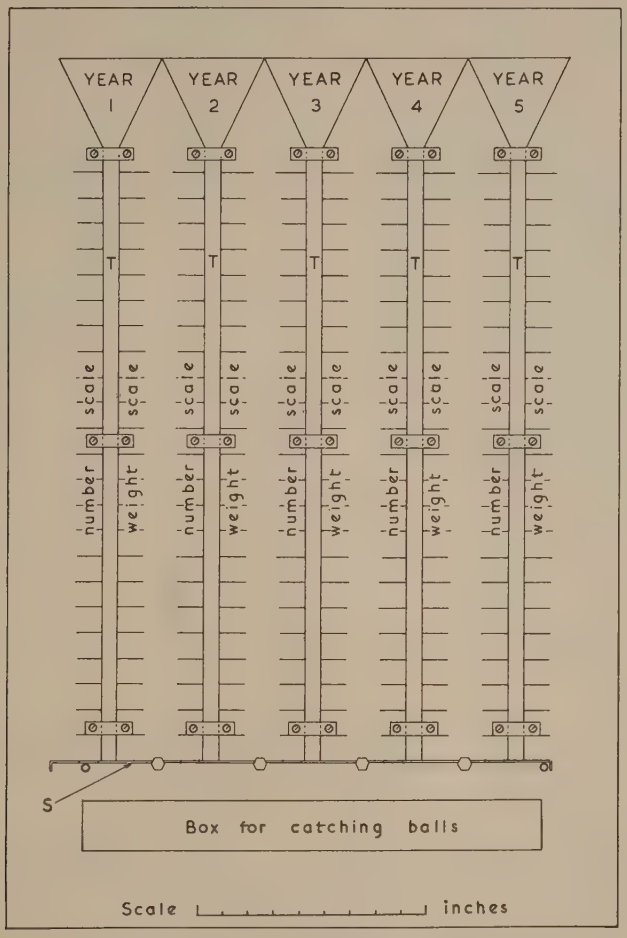

Figure 4. Method of estimating numbers of "fish" taken.

the steelyard, and can be assessed individually or in total by weights put in the pan (V).

An alternative method of assessing, when it is desired to show the numbers of "fish" in each box, is to have a series of vertical tubes across the bottoms of which there is a sliding metal strip (S), Figure 4. This metal strip has holes equal in size to the diameter of the tubes (T). By pushing the metal strip to the left the balls are held in the tubes (T). When pushed to the right the holes are brought in line with the bottom of the tubes and the balls fall into the box beneath the tubes. The balls are fed into the tubes and form a histogram of numbers, which can be read off for each year by means of a scale beside each

tube (T). On the other side of each tube a scale representing weight is placed. This scale is interchangeable with others according to the fish under investigation.

II. Method of Operation

The model can be used to demonstrate a wide range of situations occurring in exploited fish populations. Of these probably the most important, and the one for which the model was primarily designed, is the steady state yield obtainable from various fishing efforts and mesh sizes with constant recruitment. This is best shown as the yield from one year-class during its fishable life-span, which in equilibrium is the same as the catch obtained in one year from the several age-groups. To show this the slides representing fishing mortality on all five year-boxes are put in the setting appropriate to the fraction of the fish to be caught each year. The five slides representing natural mortality are similarly placed in the settings corresponding to the natural mortality. A large number of balls (the capacity is about 150) — the recruits — are then placed in the top trough and allowed to pass through the model, making their way in to one of the collecting boxes — catch (K_1), natural mortality (K_3 and K_4), and if that box is in use, survivals (K_2). The catch is then measured by the one or other system.

The essential qualities of the model and the play of the factors, can be shown most rapidly by the following sequence of actions: hang the boxes on the steelyard counterbalance; leave the weights in the pan, put the balls back into the model with the setting for fishing intensity altered by 10 per cent.; run through again and again, hang the boxes on the yard. If the load now outweighs that on the pan, we suppose that there would be a gain due to the alteration of intensity.

Alteration or yield by variation of age at first capture, as by mesh selection, is also demonstrable by putting in zero or reduced intensity of fishing in one or more of the upper boxes in the second part of the operation. Other types of demonstration may be left to the reader's imagination.

As the model does not take account of density-dependence, or of interaction with other species, it may be unwise to carry the demonstration further, without giving the necessary reservations a considerable exposition, which it is the purpose of the model to avoid. Nevertheless, the model could be used to demonstrate a variety of problems to biologists and other people whose mathematical facility would be insufficient for demonstration on paper.

III. Biased Errors in the Model

The biased errors in the model are small but are of some intrinsic interest. The model does not show the effective interaction within any one year of the fishing and natural mortality rates. When the intensity of fishing setting is high the model does not allow for actual percentage of the initial population dying of natural causes within one year being lower than with no fishing; so survival to older ages is slightly underestimated, and, therefore, yield at high intensities. The randomizing effect of the pins is not perfect. Balls starting in the trough at, say, the left side of the box are a little more likely to finish on that side. With high fishing mortality rates, the survivors of one year are concentrated on the

far ("natural mortality") side of the boxes, and hence are more likely to fall into the "natural mortality" side in the next year, which again underestimates the yield at high fishing intensities. The observer may, therefore, wish to use the last box not as, for example, "5 plus", but as "5" allowing loss of survivors (K_2) from the yield, and so to underestimate the yield at low fishing intensities, in order to counteract the bias from the two foregoing faults.

Used in that way, we believe that the model gives a fair appreciation of the principal factors in the "overfishing problem".

IV. Acknowledgement

We would like to mention M. Graham, and R. J. H. Beverton for their help in the design of the model and D. and G. Mummery who constructed the model.

V. Summary

1. A model is described which promises to be useful in illustrating the main theory of fishing dynamics.

2. Details of its construction and operation are given.

3. There is a short discussion of the biased errors in the model.

An Analysis of the Variability Associated with the Vigneron-Dahl Modification of the Otter Trawl by Day and by Night and a Discussion of its Action

by

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I. Introduction

During the early 1920's the Vigneron-Dahl modification of the otter-trawl was introduced into the British fishing industry. This modification consists essentially of putting a length of rope on each side between the otter board and the wing of the net (Fig. 1). An early description of the gear was given by Le Gall (1931). The effect of the modification is to increase the catch very considerably, and this increase has been studied by Hickling (1931) and Bowman (1932).

Hickling gives comparisons of the catches with a standard Otter Trawl (OT) and with the Vigneron-Dahl modification (VD) at the time when the hake fishery was adopting the new gear. These comparisons apply to all fish species lumped together as the original records were unfortunately destroyed, and also are based on different classes of boats though the larger and more powerful ships tended to change their gear before the smaller ones, and they fished different populations; the former working in deeper water than the latter. Furthermore the first VD trawls were of French origin and had a smaller mesh size, and Hickling gives no evidence that even later the trawls were similar (except for the bridles); in fact he states that the VD trawls had a longer and more buoyant headline. Nevertheless because his figures are based on a large area and fair length of time, they do indubitably show that the VD is more deadly, that its catching power varies enormously (Hickling gives figures for the VD catch varying from −7 to +114 per cent. greater than the OT) and that this greater catching power is related to the population density of the fish.

Bowman's data only concern the catches of haddock and are derived from two sources. He gives the results of two series of experiments during February, March, and April 1926 on board F.R.S. "Explorer" using both types of gear at

two depths (30–36 m and 110 m). Ten hours trawling was carried out at each position with each net. He states that "The cod-end meshes of the VD net were very similar in size to those of the OT", and though he does not say that the two nets were otherwise comparable, he does state that there is no appreciable difference in the selectivity of the two nets with regard to the size distribution. At the greater depth the VD gear caught 1·3 times as many haddocks as the OT and in the shallower water the catch was 2·8 times larger. BOWMAN's second source of data consists of the returns made by the Ministry of Agriculture and Fishery Measurers on board commercial vessels at the time of the change-over, and only the haddock catches from certain areas of the central North Sea are considered. The results are very similar to the experiments on "Explorer"; there is no significant difference in the size distribution of the catches of the two types of gear and the VD trawls on the average caught 50% more haddocks than the otter trawls in the same time; the range in variation of the VT/OT ratio was from 0·6 to 4·9.

Comparisons of the catches obtained with different designs of trawls have been made by MARGETTS (1949a) and PARRISH (1949 and 1951). MARGETTS (1949b) has also compared the fishing capacities of trawlers and Danish-seiners.

MARGETTS (1949a) makes paired comparisons in the catches of different trawls on different ships. One series of experiments compares a VD trawl on board "Sir Lancelot" and an OT on "Explorer". This series is also the basis of PARRISH's (1951) more detailed analysis. While the spread of the net was greater on "Explorer", the 30 fathom bridles on "Sir Lancelot" resulted in a greater spread between her otter boards. It was found that "Explorer" caught more haddock and whiting and "Sir Lancelot" more bottom fish — skate and flatfish. These differences were explained by the make-up of the nets though MARGETTS does say, "It is also conceivable that the greater catches of large haddock by the 'Lowestoft' trawl with Vigneron-Dahl modifications, on "Sir Lancelot" as compared with the 'Aberdeen' trawl, (on "Explorer"), were due to difference in the behaviour of different sizes of haddock in relation to the action of the bridles as well as to the mesh effect discussed above". HICKLING also found that VD gear caught more of the larger hake. In the analyses of variance of the "Explorer"/"Sir Lancelot" data PARRISH (1951) did not consider the haul to haul variability of each net separately, nor even the within hauls variance for all the data though this may easily be got from his tables.

The variability between hauls using the same gear over the same ground has, however, been studied by BARNES and BAGENAL (1951) and by TAYLOR (1953). BARNES and BAGENAL, using a VD trawl in the Clyde area, analysed "round fish" and "flatfish plus *Nephrops*" separately and found that for both groups the coefficient of variation varied from 40% to 85%. TAYLOR discusses the statistical distributions of the catches from Georges Bank, Newfoundland, and concludes that the catch per tow conforms to the negative binomial and that the distribution of species and numbers of individuals represented by each, fits a logarithmic series satisfactorily, and the occurrence of species in successive tows to have a Poisson distribution. TAYLOR points out that these distributions are self-consistent and that "the variance may be reduced, and the amount of information increased by decreasing the size of the observed mean, and it is suggested that this may be accomplished by reducing the length of tow and by reducing the size of the trawl net".

In view of TAYLOR's remarks I thought the variability of the VD and OT

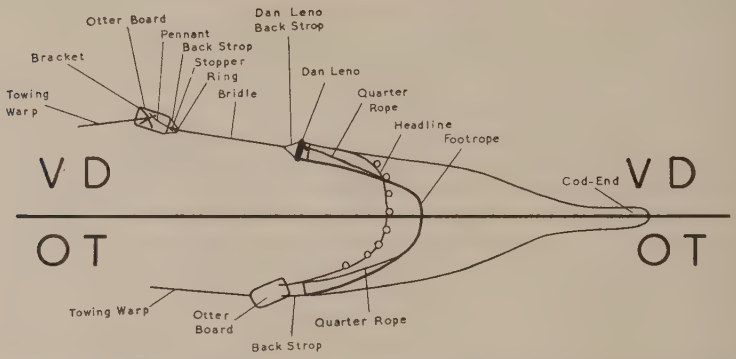

Figure 1. Diagram to illustrate the parts of a trawl and the names used in the text. In the lower half of the diagram the gear is rigged as an Otter Trawl while the upper half illustrates the Vigneron-Dahl modification with bridles.

should be examined and that a more exact estimate of the catching power of the VD modification should be made with all other details of the gear remaining constant. It was also evident that the behaviour of the fish in relation to the bridle of the VD trawl (or for that matter the bridles of a seine net) is of extreme importance in understanding what aspect of the gear leads to the fish entering the net. MARGETTS (1949) makes the suggestion that "The action of the legs and Vigneron-Dahl bridles is presumably rather like that of seine net warps, driving fish towards the ground to be swept by the net", and later (1952) he discusses possible ways in which this may happen. A less likely hypothesis would be to suppose that the OT only catches a small proportion of the fish in the path of the net, and that the rest are scared away primarily by the advancing otter boards. The greater catches with the VD gear could now be explained by the boards being further away and so scaring the fish less. The objection to this hypothesis is that a separate one is now needed to explain how a seine net works.

Of the senses that we may suppose fish to possess, we can rule out the possibility that they perceive the bridles by smell, touch, or taste and consider the possibilities of sight and hearing. Hearing in this paper will be considered to be the ability to perceive vibrations of all wavelengths ranging from our supersonic to low frequency waves that are "felt" rather than heard. The ability to perceive low frequency waves has been discussed by PUMPHREY (1950) who concludes that the lateral line of fish would appear to be admirably suited for their perception and for the accurate location of the source of vibrations. This ability would seem well suited for the perceiving of the bridles of a VD trawl or of a seine net. With regard to the possibility of fish seeing the on-coming bridles, there is little published evidence that helps to give positive information on the minimum amount of light needed by British commercial species to be aware of their environment. It must be remembered that very little light is available in many of the places where a VD trawl is successful, as for instance at 300 fathoms SW of Ireland. It was decided that the effect of light on the working of a VD trawl might be examined by comparing catches with and without bridles by day and by night, and that simple experiments of this kind

Table 1

Specifications of the trawl with 54 foot headline and 72 foot footrope used on M.F.V. "Calanus"

SQUARE 140/112/10 ft. 150s Twine 5″ mesh
Set up 140 meshes and braid 2 double rows. Continue in single twine and bate every 3rd row. After last bating add plain rows to make length 10 ft.

TOP WINGS 50/8/24 ft. 150s Twine 5″ mesh
Each wing is 40 meshes single and 10 double. Double corners 10 to 0. Flymeshes on inner selvedge. 4 double rows in end of wings.

LOWER WINGS 112/16/38 ft. 125s Twine 5½″ mesh
Set up 112 meshes and braid 3 double rows. Each wing is 20 meshes single and 10 double. Double corners 10 to 0. Flymeshes on inner selvedge.
Crease every 3rd row to 16 meshes wide. Put in one double row, then crease every 2nd row to end.
Creases on selvedge.
6 double rows in end of wings.

BELLY 112/80/19 ft. 125s Twine
One double row at top.

3 batings every 7th row	.....	5 ″ mesh	}	Average 4·19″
3 – – – –	.....	4½″ mesh		
4 – – 6th –	.....	4 ″ mesh		
6 – – 7th –	.....	3½″ mesh		

COD-END 80/50/4½/12 ft. 125s Twine 3½″ mesh
80/50 Double twine.
Bate every 2nd row.
50/50 Double twine.
No batings.
Finish 12 ft. long from last bating.

HEADLINE
23 ft. each wing, 8 ft. bosom, made from 3″ 4 std. manila or sisal.

FOOTROPE
30 ft. each wing, 12 ft. bosom, made from 2″ 6/12s steel wire, rounded, with 3″ sisal on wings, and 4″ coir on bosom.

BACK STROPS 2½″ 8 ft. DAN LENO STROPS Headline, 1½″ 10 ft. Footrope, 2″ 10 ft.

BRIDLES 2½″ 15 fathom. DAN LENOS 2½ ft. × 4″ × 4″ wooden posts.

would provide direct evidence, since if the fish are frightened by the sight of the bridles, under extremely poor lighting conditions at night the effect of the bridles should be smaller. The possibility that the gear would be visible because of phosphorescence cannot be ruled out completely, and although on some dates (25. Aug. 1952) phosphorescence was observed at the surface, at other time (31. Oct. 1957) none was seen.

II. The Gear, Ground, and Method of Working

A standard type of trawl was used as supplied by the Gourock Rope Works, the detailed specifications are given in Table 1, and Figure 1 illustrates the names used for the various parts of the gear. When using the VD gear, the

Table 2

Details of the experimental design in Series A, times GMT

Haul No.		I	II	III	IV	V	VI	VII	VIII
25. Aug. 52...	Gear	OT	VD	VD	OT	OT	VD	VD	OT
Sunset	Shot	1600	1725	1815	1930	2130	2248	0002	0117
19·03.....	Hauled	1630	1755	1845	2000	2200	2318	0032	0147
1. Sept. 52	Gear	OT	VD	VD	OT	OT	VD	VD	OT
Sunset	Shot	1239	1340	1435	1543	2030	2130	2315	0015
18·48.....	Hauled	1309	1410	1505	1613	2100	2200	2345	0045
27. Apr. 53....	Gear	VD	OT	OT	VD	VD	OT	OT	VD
Sunset	Shot	1400	1502	1549	1740	2050	2227	2345	0044
19·15.....	Hauled	1430	1532	1619	1810	2120	2257	0015	0114
4. May 53.....	Gear	VD	OT	OT	VD	VD	OT	OT	VD
Sunset	Shot	1405	1505	1550	1643	2117	2255	2340	0038
19·26.....	Hauled	1435	1535	1620	1713	2147	2325	0010	0108
31. Oct. 57....	Gear	VD	OT	OT	VD	VD	OT	OT	VD
Sunset	Shot	0934	1044	1142	1346	2012	2144	2345	0110
16·43.....	Hauled	1004	1114	1212	1416	2042	2214	0015	0140

quarter rope went to a becket on the dan leno, but when using the OT gear it went to another becket on the bracket of the otter board, the other end of the quarter rope ran direct to the footrope and not through beckets on the headline. There was no tickler chain nor any bobbins on the footrope. When a change-over from VD to OT gear was made, the back strops on the otter board were unshackled from the ring and shackled directly to the wing of the trawl. Thus the gear in both cases was exactly the same except that the OT gear lacked the pennants, stoppers, rings, bridles, dan lenos, and dan leno strops. The dan leno strops on each side were shackled to the top and bottom of the wing of the net and ran through holes in the dan leno and were shackled together to the after end of the bridle. This gear, with and without the VD modification, was shot and hauled in the usual manner from M. F. V. "Calanus" under the supervision of Captain R. E. SOUTER. Great care was taken to ensure that the trawl hauls should be as comparable as possible in all respects other than the VD modification. Each haul, where space allowed (as in the main channel to the west of the Isle of Cumbrae), was made on a somewhat elliptical course, starting and returning to approximately the same position. In the Largs Channel (to the east of the island) the hauls were made in straight line northwards from the Fairlie Buoy. Positions were also checked from conspicuous objects on the shore, and from street and other lights at night. During each set of hauls echo-soundings were taken continuously and these were used as a further check that the trawl hauls were consistently taken over similar ground. There was considerable variation in the weather on the dates when the hauls were taken. The mean wind speeds around noon and midnight are given in an appendix, Table 17; but it should be borne in mind that the Clyde is a sheltered area.

Two series of experiments were carried out. Series A was primarily designed to show if the VD modification has a similar effect by night as it has by day. Series B was planned to give more evidence on the variability in replicate catches of the VD and OT trawls under comparable conditions. Each series consisted of hauls taken on five different dates. Details are given in Tables 2 and 3.

Table 3

Details of experimental design in Series B, times GMT

Haul No.		I	II	III	IV
29. Oct. 56	Gear	VD	OT	OT	VD
	Shot	1029	1140	1318	1417
	Hauled	1059	1210	1348	1447
30. Oct. 56	Gear	VD	OT	OT	VD
	Shot	1017	1115	1309	1407
	Hauled	1047	1145	1339	1437
31. Oct. 56	Gear	VD	OT	OT	VD
	Shot	1001	1116	1246	1340
	Hauled	1031	1146	1316	1410
1. Nov. 56	Gear	VD	OT	OT	VD
	Shot	1005	1116	1248	1340
	Hauled	1035	1146	1318	1410
2. Nov. 56	Gear	VD	OT	OT	VD
	Shot	1005	1101	1248	1343
	Hauled	1035	1131	1318	1413

In all cases the hauls were of $\frac{1}{2}$ hr. duration, the time taken from when the warps were "all square aft" in the towing block to the time they knocked out again, that is from "blocking up" to "knocking out".

III. The Collection and Analysis of the Data

The numbers of each species of fish caught were obtained from each haul and a note taken of the invertebrates and amount of weed (*Laminaria*) present. The details of the fish caught are given in Tables 4 and 5, and the scientific names in the appendix Table 16.

Following the practice of BARNES and BAGENAL (1951) and PARRISH (1951), and the theory given by TAYLOR (1953), the statistical analysis was carried out after the logarithmic transformation, $y = \log (x + 1)$.

Analyses of variance and tests of significance were carried out on the transformed date treating each species in each series separately.

Series A

On five widely separated occasions a set of experiments was carried out, four hauls being taken by day and four by night. These four hauls consisted of two with OT and two with VD gear and it was arranged that the first and last hauls were taken with similar gear. In the analyses of variance there were therefore two main sources of variation, due to different Times (day and night), and due to different Gear (OT and VD). The first order interaction, T $\times$ G, is of importance since it tests if the greater catches with the VD gear were similar by day and night, which was one of the main purposes of the experiments. An example of the analyses of variance tables for the catches of cod in Series A is given in Table 6 and the results for all species caught in adequate numbers are given in Table 7. The third analyses were designed to show the variability between the hauls within the same gear. With both the OT and the VD gear, by day and by

Table 4

Details of actual catch in Series A

Haul No.	I	II	III	IV	V	VI	VII	VIII
Date 25. Aug. 1952								
Cod	4	11	8	1	2	3	4	–
Haddock	58	318	263	8	3	13	25	1
Whiting	128	162	140	12	1	26	23	19
Saithe	2	–	–	–	–	–	–	–
Hake	2	2	3	–	–	2	–	–
Mackerel	2	26	6	1	–	–	–	–
Gurnard	–	3	3	–	–	–	–	–
Angler	–	1	–	–	–	–	–	–
Plaice	5	12	35	3	4	7	4	1
Witch	–	32	52	3	2	51	28	–
Lemon Sole	1	2	3	–	–	1	1	–
Long Rough Dab	30	91	76	25	6	18	26	5
Spurdog	24	119	184	17	–	2	3	–
Thornback Ray	–	1	–	–	–	2	1	–
Total	256	780	773	70	18	125	115	26
Date 1. Sept. 1952								
Cod	–	5	6	2	–	3	5	–
Haddock	75	428	355	26	1	112	40	6
Whiting	10	24	16	4	1	9	16	1
Poor Cod	–	1	1		–	–	–	–
Norway Pout	–	3	–	1	–	–	–	–
Saithe	1	–	–	1	–	–	–	–
Hake	–	6	2	–	–	2	–	–
Argentine	–	–	2	–	–	1	–	–
Gurnard	–	1	5	1	–	–	–	–
Angler	–	1		–		–	–	–
Conger	–	–	–	–	–	1	1	–
Plaice	–	32	18	–	2	16	7	5
Witch	2	76	62	3	–	55	41	4
Lemon Sole	–	2	3	–	–	3	–	–
Common Dab	–	1	–	–	–		–	–
Long Rough Dab	15	145	128	18	5	33	46	17
Spurdog	19	54	89	2	1	4	7	3
Thornback Ray	–	1	3	–	–	4	1	–
Cuckoo Ray	–	2	–	–	–	–	–	–
Total	122	782	690	58	10	243	164	36
Date 27. Apr. 1953								
Cod	17	1	5	20	7	1	5	15
Haddock	902	136	148	212	12	–	18	23

Haul No.	I	II	III	IV	V	VI	VII	VIII
Whiting	95	18	6	30	3	–	6	19
Poor Cod	1	–	–	–	–	–	–	1
Norway Pout	–	–	–	–	–	–	–	1
Hake	1	–	–	1	1	–	–	–
Gurnard	30	4	2	2	–	–	–	–
Conger	–	–	–	1	–	–	–	–
Plaice	86	1	9	96	15	2	7	20
Witch	52	3	7	98	25	2	2	25
Lemon Sole	2	–	–	1	–	–	–	–
Common Dab	1	–	–	–	–	–	–	–
Long Rough Dab	15	4	1	23	8	2	3	8
Spurdog	–	–	–	–	–	–	1	–
Thornback Ray	1	1	–	–	–	–	–	–
Total	1203	168	178	484	71	7	42	112
Date 4. May 1953								
Cod	17	1	1	36	11	1	1	5
Haddock	595	56	38	460	10	2	10	13
Whiting	138	32	10	346	10	12	5	4
Poor Cod	–	–	–	1	–	–	–	1
Ling	–	–	–	–	–	–	–	1
Hake	2	–	–	2	1	–	–	–
Gurnard	18	–	2	10	–	–	1	1
Conger	–	–	–	–	1	–	1	2
Plaice	78	3	4	70	24	6	3	14
Witch	30	1	4	34	20	1	2	20
Lemon Sole	–	1	–	1	1	–	–	–
Long Rough Dab	48	3	5	63	11	4	5	5
Spurdog	44	3	1	17	2	–	–	6
Thornback Ray	–	–	–	–	–	–	–	2
Total	970	91	65	1040	91	26	28	74
Date 31. Oct. 1957								
Cod	8	–	–	8	5	2	1	1
Haddock	387	11	5	348	22	4	6	3
Whiting	2	–	1	–	–	1	–	–
Norway Pout	–	–	–	1	1	–	–	–
Hake	–	–	–	–	–	–	–	1
Conger	–	–	–	–	1	–	–	–
Plaice	42	–	–	28	40	5	–	37
Witch	3	–	–	2	2	2	–	5
Lemon Sole	1	–	–	–	–	–	–	–
Long Rough Dab	27	1	–	9	3	3	2	7
Thornback Ray	2	–	–	–	–	–	–	1
Nurse Hound	2	–	–	1	–	1	–	–
Total	474	12	6	397	74	18	9	55

Table 5

Details of actual catches in Series B

Haul No.	I	II	III	IV	Haul No.	I	II	III	IV
Date 29. Oct. 1956					Witch	22	1	–	34
Cod	28	6	8	11	Common Dab.	3	1	–	2
Haddock	120	36	34	48	Long Rough Dab.	10	2	2	22
Whiting	10	3	2	6	Spurdog	3	–	–	–
Hake	8	–	1	5	Thornback Ray	2	–	–	–
Argentine	1	–	–	1	Spotted Ray	–	–	–	1
Plaice	81	–	1	50					
Witch	86	1	2	27	Date 1. Nov. 1956				
Long Rough Dab.	41	2	1	18	Cod	11	1	2	13
Lemon Sole	2	–	–	2	Haddock	163	5	10	108
Spurdog	5	–	–	–	Whiting	34	4	9	4
Thornback Ray	1	–	–	–	Hake	7	–	–	4
					Norway Pout	–	1	2	–
Date 30. Oct. 1956					Gurnard	1	–	–	–
Cod	19	20	3	13	Plaice	74	1	–	41
Haddock	115	20	10	77	Witch	51	–	1	42
Whiting	16	6	5	3	Lemon Sole	–	–	–	3
Hake	6	–	–	6	Common Dab.	1	–	–	1
Norway Pout	1	–	–	3	Long Rough Dab.	29	2	–	14
Gurnard	1	–	–	1	Spurdog	3	–	–	–
Argentine	–	–	–	1	Spotted Ray	1	–	–	1
Mackerel	1	–	–	–					
Plaice	59	–	1	25	Date 2. Nov. 1956				
Witch	43	2	1	34	Cod	14	2	2	24
Lemon Sole	–	–	–	2	Haddock	76	9	17	57
Common Dab.	–	1	–	1	Whiting	25	10	17	5
Long Rough Dab.	19	3	3	27	Hake	5	–	1	3
Spurdog	2	–	1	1	Norway Pout	–	2	–	–
Thornback Ray	–	–	–	1	Saithe	–	–	2	–
					Gurnard	1	–	–	–
Date 31. Oct. 1956					Argentine	–	–	–	1
Cod	21	–	2	20	Plaice	25	–	2	27
Haddock	118	20	15	173	Witch	16	–	–	27
Whiting	16	12	1	9	Lemon Sole	3	–	–	1
Hake	5	1	–	8	Common Dab.	1	–	–	1
Norway Pout	–	–	1	–	Long Rough Dab.	14	3	2	26
Saithe	–	1	2	–	Spurdog	1	–	1	2
Gurnard	1	–	–	1	Thornback Ray	–	–	1	2
Argentine	1	–	–	–	Cuckoo Ray	1	–	–	–
Plaice	39	–	2	57	Spotted Ray	–	–	–	1

night, there were two replicate hauls. (See Table 2, 25. Aug. 52. OT; day, hauls I and IV; night hauls V and VIII; VD; day, hauls II and III; night, hauls VI and VII.) The variances for these pairs were calculated and the sum of the "between hauls within gear" variances for each gear by day and night equalled the residual in the second analyses of variance. The coefficient of variation, C, for each kind of gear was calculated from

$$C = \sqrt{\text{antilog}\,(\sigma^2/\log e)} - 1$$

which is a rearrangement of equation (5) of BAGENAL (1955) and where σ^2

Table 6

Example of the analyses of variance table in Series A; for cod on 25. August 1952

Source	Sums of squares	Degrees of freedom	Mean square	Variance ratio	Significance
T	·196878	1	·196878	3·83	N.S.
G	·431056	1	·431056	8·39	*
T × G	·005461	1	·005461	–	–
Residual	·205483	4	·051371		
Total	·838878	7			

Table 7

Results of analyses of variance of hauls taken in Series A

Date	Source	Cod	Haddock	Whiting	Plaice	Witch	Long Rough Dab	Spurdog
24.	T	N.S.	*	N.S.	N.S.	–	* *	* *
Aug.	G	*	*	N.S.	*	* *	* *	* *
1952	T × G	–	–	–	N.S.	–	–	–
1.	T	N.S.	*	*	N.S.	–	* *	*
Sept.	G	* *	* *	* *	* *	* *	* *	*
1952	T × G	N.S.	–	N.S.	*	–	N.S.	–
27.	T	–	*	N.S.	N.S.	*	N.S.	
April	G	N.S.	N.S.	N.S.	*	* *	* *	
1953	T × G	–	–	–	N.S.	–	N.S.	
4.	T	N.S.	N.S.	*	*	N.S.	*	*
May	G	* *	*	N.S.	* *	* *	* *	* *
1953	T × G	N.S.	N.S.	*	*	–	* *	N.S.
31.	T	–	*		N.S.	N.S.	–	
Oct.	G	*	*		* *	*	*	
1957	T × G	*	*		–	–	N.S.	

* * indicates significance at 1% probability level.
* indicates significance at 5% probability level.
N.S. indicates not significant.
– indicates mean square less than that against it is tested.

equals the "between hauls within gear" variance. The variances and the coefficient of variation based on the mean variance, are shown in Table 8.

Series B

This series consisted of five replicate experiments made over five consecutive days from 29. October to 2. November 1956. An analysis of variance similar to that for Series A was carried out, the main effects being Days, Gear, and Hauls. If the Hauls variance and its interaction were non-significant, their sums of squares were pooled with the second order interaction, and the main effects and the "Days × Gear" interaction were tested against this error variance. An example of the analyses of the haddock catches is given in Tables 9 and 10 and the results for all species caught in adequate numbers are given in Table 11.

Table 8

The "between hauls within gear" variances, and the coefficients of variation for Series A

Otter Trawl	Mean variance Day	Mean variance Night	Coefficient of variation (%) Day	Coefficient of variation (%) Night
Cod	·064322	·060754	37·50	37·15
Haddock	·098911	·236179	41·11	59·14
Whiting	·190977	·228365	52·46	57·93
Plaice	·088164	·093641	39·95	40·53
Witch	·078379	·097463	38·94	40·95
Long Rough Dab	·029138	·044950	34·16	35·62
Spurdog	·127194	·045300	44·31	35·67

Vigneron-Dahl Trawl	Mean variance Day	Mean variance Night	Coefficient of variation (%) Day	Coefficient of variation (%) Night
Cod	·012257	·044911	32·66	35·62
Haddock	·042227	·092534	35·37	40·41
Whiting	·050801	·208321	36·18	54·94
Plaice	·028694	·021284	34·12	33·45
Witch	·014218	·017074	32·83	33·09
Long Rough Dab	·025298	·022390	33·82	33·57
Spurdog	·031428	·054443	34·37	36·54

Table 9

Example of first analysis of variance table for haddock in Series B

Source	Sums of squares	df	Mean square	F	Significance
Days	·198049	4	·0495		
Gear	3·090419	1	3·0904		
Hauls	·018362	1	·0184	–	–
D × G	·439080	4	·1098		
D × H	·083127	4	·0208	–	–
G × H	·039681	1	·0397	1·91	N.S.
D × G × H	·083438	4	·0208		
Total	3·952156	19			

Table 10

Example of second analysis of variance table for haddock in Series B

Source	Sums of squares	df	Mean square	F	Significance
Days	·198049	4	·0495	2·21	N.S.
Gear	3·090419	1	3·0904	137·96	* *
D × G	·439080	4	·1098	4·88	*
Residual	·224608	10	·0224		
Total	3·952156	19			

Table 11

Results of analyses of variance of hauls taken in Series B

Source	Cod	Haddock	Whiting	Hake	Plaice	Witch	Long Rough Dab
Days.....	N.S.	N.S.	–	–	–	N.S.	–
Gear.....	* *	* *	N.S.	* *	* *	* *	* *
Hauls....	–	–	N.S.	–	N.S.	–	–
D × G...	N.S.	*	–	–	–	–	–
D × H...	N.S.	–	–	–	N.S.	–	N.S.
G × H...	–	N.S.	N.S.	–	*	–	N.S.

Table 12

The ratios of day/night catches for OT and VD gears separately and combined in Series A

	25. August 1952			1. September 1952		
	VD	OT	Total	VD	OT	Total
Cod	2·71	2·50	2·67	∞	∞	∞
Haddock	15·29	16·50	15·40*	5·15	14.43	5·56*
Whiting	6·16	7·00	6·41	1·60	7·00	2·00*
Plaice	4·27	1·60	3·44	2·17	0	1·67
Witch	1·06	1·50	1·07	1·44	1·25	1·43
Long Rough Dab	3·80	5·00	4·04**	3·46	1·50	3·03**
Spurdog.....	60·60	∞	68·80**	13·00	5·25	10·93

	27. April 1953			4. May 1953		
	VD	OT	Total	VD	OT	Total
Cod	1·68	1·00	1·54	3·31	1·00	3·06
Haddock	31·83	15·78	26·38*	45·87	8·00	32·83
Whiting	5·68	4·00	5·32	34·57	2·47	16·97*
Plaice	5·20	1·11	4·36	3·89	0·78	3·30*
Witch.....	3·00	2·50	2·96*	1·60	1·67	1·60
Long Rough Dab	2·38	1·00	2·05	6·94	0·89	4·76*
Spurdog.....	–	–	–	7·63	∞	8·13*

	31. October 1957		
	VD	OT	Total
Cod	2·67	0	1·78
Haddock	29·40	1·60	21·46*
Whiting	–	–	–
Plaice	0·91	0	0·85
Witch.....	0·71	0	0·56
Long Rough Dab	3·60	0·20	2·47
Spurdog.....	–	–	–

∞ does not necessarily indicate a large catch by day, but does indicate that no fish were caught at night. 0 indicates that there was no daytime catch, and – that there were insufficient fish to analyse. * * indicates that the day and night catches were significantly different at the 1% level and * indicates significance at the 5% level.

Table 13

The "between hauls within gear" variances and the coefficients of variation for Series B

Dates, 1956	29. Oct.	30. Oct.	31. Oct.	1. Nov.	2. Nov.	Mean	% C
OTTER TRAWL							
Cod	·005940	·259200	·113764	·015488	·000000	·078878	38·97
Haddock	·000288	·039480	·006962	·034584	·000000	·016263	33·02
Whiting	·007812	·002244	·330484	·045300	·022898	·081748	39·27
Hake	·045301	–	·045301	–	·045301	·045301	31·00
Plaice	·045301	·045301	·113764	·045301	·113764	·072686	32·23
Witch	·015488	·015488	·045301	·045301	–	·030395	34·28
Long Rough Dab	·015488	·000000	·000000	·113764	·007812	·027413	34·00
VIGNERON-DAHL TRAWL							
Cod	·073344	·012012	·000200	·002244	·024642	·002248	33·57
Haddock	·077224	·014964	·013612	·015842	·024642	·029257	34·18
Whiting	·019208	·197192	·026450	·357012	·202884	·160549	48·40
Hake	·015488	·000000	·015488	·020808	·015488	·013454	32·77
Plaice	·021218	·065884	·012960	·031752	·001512	·026665	33·94
Witch	·121524	·005000	·016562	·003362	·023544	·033998	34·62
Long Rough Dab	·059168	·010658	·051520	·045300	·032512	·039832	35·14

IV. Results

A. Catches by day and by night

It is clear from Table 4 where the actual numbers of all species of fish caught in Series A are given, that the daytime catches are usually many times greater than those obtained at night. This applies to all species and the ratios of day/night catches for all numerous species are given in Table 12. The statistical significance of the greater daytime catches, which was determined in the analyses of variance, is indicated by asterisks (as in Table 6). There was no evidence in the catches themselves to indicate why there should be these differences, and as fishermen know well, in some regions the difference is reversed; the greater catches being taken by night. A vertical migration of fish traces was not seen on the echo-sounder, but traces of bottom-living fish have rarely been convincing on this individual machine.

HICKLING (1931) found that the efficiency of the VD gear was proportional to the population density. From the figures analysed here it appears that the VD modification works as well by night, when the catches were low, as by day when they were higher.

B. Comparison of the variability of hauls with OT and VD trawls

The variances of the pairs of replicate hauls taken by day and by night in Series A are given for each kind of gear in Table 8, as well as the coefficients of variation. The same parameters for the Series B data are given in Table 13.

In Series A, the day hauls were usually less variable than the night hauls, the averages of the coefficients of variation being about 6·7% lower in the day hauls. Furthermore the coefficients of variation for the OT tended to be higher than those for the VD gear; "C" being highest with the OT by night and lowest with the VD by day. Thus there was a greater variability with the smaller catches (cf. TAYLOR, 1953). However, the differences between the coefficients for

the two gears, though consistent, is only small, averaging 3–4%, and in Series B the differences are reversed; the VD gear with its larger catches were on the whole a little more variable. It seems therefore that these differences are unlikely to be significant and we may conclude that the bridles of the VD trawl do not significantly affect the variability in the catch.

In both Series A and B the variability was less than was expected from the results of BARNES and BAGENAL (1951) who found that the coefficient of variation varied from 40 to 85% and they took 75% as a representative value. They do, however, give coefficients of variation of 27–51% for THOMPSON's (1928) haddock results and 25 to 88% for HICKLING's (1933) with hake. BAGENAL (1955) showed that the methods of BARNES and BAGENAL gave too large a coefficient of variation, the discrepancy ranging from 2% for C = 20% to 15% for C = 60%. The coefficients given in Tables 7 and 12 range from 30% to 60% and we may take 40% as a representative value.

C. The effect of VD bridles on the catch

The ratios of VD/OT for Series A and B are given in Tables 14 and 15. The statistical significance of each increased catch with the VD gear over the corresponding OT catch is indicated by asterisks. Bearing in mind that the bridles were only 15 fms long, the VD gear caught considerably more than HICKLING's (1931) or BOWMAN's (1932) results would lead one to expect. On each occasion and for each species, the increase with VD gear is truly remarkable. The ratios showing the increased catches when using bridles do of course only apply to this particular trawl used under the same conditions of towing speed, etc. Whether a trawl is successful at catching flatfish or round fish depends to a large extent on how the footrope rides over the bottom and how the headline and footrope take the towing strain (MARGETTS, 1949a). There is probably little doubt that if bridles were put on an OT that was more efficient at catching flatfish, their effect would not be so spectacular. However, the purpose of these experiments was to see to what extent the effect of the bridles was consistent (i. e., had a low coefficient of variation) and to see if the effect was as great by night as by day. It is clear from Table 14 that the bridles are effective in the dark, and since in the analysis of variance results (Table 7) the first order interaction "G × T" were rarely significant, even at the 5% probability level, we are justified in saying that this effectiveness did not differ by night and by day.

V. Discussion

The results given above show that somehow the fish perceive the bridles and are scared by them into the path of the net. There is little evidence on the extent to which the bridles are in contact with the bottom, but although they are sometimes rubbed clean, on M. F. V. "Calanus" this is a rare occurrence, and it seems that they certainly do not always touch the bottom, and certainly do not on level ground (Anon. 1952, Ministry of Agriculture and Fisheries film "Trawls in Action" and MARGETTS 1952, Fig. 3). MARGETTS (1952) writes "The question still remains, however, how do bridles work? We know that they allow a greater spread between the otter boards and drive fish inwards into the path of the oncoming net. This may be due to their disturbance of the

Table 14

The ratios of VD/OT catches, by day and by night separately and combined in Series A

	25. August 1952			1. September 1952		
	Day	Night	Total	Day	Night	Total
Cod	3·80	3·50	3·71*	1·37	–	1·37**
Haddock	8·80	9·50	8·84*	7·75	21·71	8·66**
Whiting	2·16	2·45	2·19	2·86	12·50	4·06**
Plaice	5·88	2·20	4·46*	∞	3·29	10·43**
Witch	28·00	39·50	32·60*	27·60	24·00	26·00**
Long Rough Dab	3·04	4·00	3·20**	8·27	3·59	6·40**
Spurdog	7·39	∞	7·51**	6·81	2·75	6·16*

	27. April 1953			4. May 1953		
	Day	Night	Total	Day	Night	Total
Cod	6·17	3·67	4·92*	26·50	8·00	17·25**
Haddock	3·92	1·94	3·80	11·22	1·92	10·17*
Whiting	5·21	3·67	4·90	11·52	0·82	8·44
Plaice	18·20	3·89	11·42*	21·14	4·22	11·63**
Witch	15·00	12·50	14·29*	12·80	13·33	13·00
Long Rough Dab	7·60	3·20	5·40**	13·88	1·78	7·47**
Spurdog	–	–	–	15·25	∞	17·25**

	31. October 1957		
	Day	Night	Total
Cod	∞	2·00	7·33*
Haddock	45·94	2·50	29·23*
Whiting	–	–	–
Plaice	∞	15·40	29·40**
Witch	∞	3·50	6·00*
Long Rough Dab	36·00	2·00	7·67*
Spurdog	–	–	–

∞ Does not necessarily indicate a large VD catch, but indicates that no fish were caught with the OT gear. 0 would indicate that no fish caught with the VD trawl, and, – that there were insufficient fish to analyse. **indicates that the VD and OT catches were significantly different at the 1% probability level and * indicates significance at the 5% level.

Table 15

The ratios of VD/OT for the catches in Series B

Dates, 1956	29. Oct.	30. Oct.	31. Oct.	1. Nov.	2. Nov.	Ratios of totals
Cod	2·79	1·39	20·50	8·00	9·50	3·78 * *
Haddock	2·40	6·40	8·31	18·07	5·12	5·99 * *
Whiting	3·20	1·73	1·92	2·92	1·11	1·86N.S.
Plaice	131·00	84·00	48·00	115·00	26·00	68·29 * *
Witch	37·67	25·67	56·00	93·00	∞	47·75 * *
Long Rough Dab	19·67	7·67	8·00	26·50	8·00	11·00 * *
Hake	13·00	∞	13·00	∞	8·00	19·00 * *

∞ does not necessarily indicate a large VD catch, but indicates that no fish were caught with the OT gear.

* * indicates that the VD and OT catches were significantly different at the 1% probability level.

bottom, in which case, as explained above, they should not work on really flat grounds. It may be due to the disturbance of the bottom or the turbulence of the water caused by the otter boards — fish would probably feel the sand in the widening cloud behind the otter boards against their bodies as the frogmen did, and would doubtless become aware of unusual water movements. It may be due to fish seeing the bridles or sand clouds, although this is unlikely at great depths in water that is none too clear. Or it may be due to the vibrations which the gear must set up and which may well be detected or heard by the fish. When these possibilities are considered together with the effects of the use of ropes in seining and pelagic trawling it would seem that the vibration or water-disturbance theories, either separately or together, appear to provide the more likely explanation".

It would seem that once the fish is behind the otter boards and bridles, where the widening cloud of sand is, it has already escaped capture. Furthermore, if one considers hearing in fish to be the ability to perceive vibrations of all wave-lengths ranging from the human super-sonic to low frequency waves that are "felt" rather than heard, the water-disturbance and vibration theories are the same. The possibility that fish see the oncoming bridles at night at 30–40 fms is very remote. The only feasible explanation would seem to be that the fish are driven by vibrations set up by the bridles passing through the water, and at times over the bottom.

It should be possible to reproduce such vibrations artificially, and if they could be directed in a beam or an arc from vibrators on a ship it should be possible to drive fish from areas of rough ground to where they could be more easily caught or to keep them in sheltered bays by means of shore-based vibrators on the headlands. The attempts that have been made in the past to scare and guide fish with sound waves (for example, BURNER and MOORE, 1953, and MOORE and NEWMAN, 1956) have shown that fish perceive a wide range of frequencies, but that they do not continue to move from a stationary sound source. The nature of the vibrations set up by VD gear bridles should first be analysed and made reproducible, and then if the other practical problems can be overcome, a very great advance in fishing technique might be made.

VI. Summary

1. Two series of experiments were carried out to investigate the action of the bridles of a Vigneron-Dahl trawl and the variability in catch that may be associated with them.

2. Series A consisted of five experiments when eight half-hour hauls were taken, four by day and four by night. At both times two of the hauls were with bridles (VD) and two without (OT). Series B consisted of four daytime hauls with and without bridles taken on each of five consecutive days.

3. Analyses of variance were carried out on the numbers of fish caught after a logarithmic transformation. From these analyses the significance of the differences in the catches was found.

4. The daytime catches were consistently and statistically significantly greater than those taken at night but the reason for this remains unknown. With the VD trawl the bridles do not appear to affect the variability in the catch although the numbers caught are significantly greater. The important point that emerges from Series A is that the bridles of the VD gear increase the catch by night in

the same way as they do by day. This is shown in the analyses of variance tables where the Gear × Time interaction is only rarely significant, and it is taken to indicate that the possibility that fish see the bridles can be ruled out.

5. From a general discussion of how the fish perceive the VD gear it is concluded that they feel the vibrations set up by bridles as they pass through the water and over the bottom. It suggested that if these vibrations could be produced artificially a very great advance in fishing technique would be possible.

APPENDIX

Table 16

Scientific names of fishes mentioned

Cod	*Gadus callarias* L.
Haddock	*Gadus aeglefinus* L.
Whiting	*Gadus merlangus* L.
Poor Cod	*Gadus minutus* L.
Norway Pout	*Gadus esmarkii* Nilsson
Saithe	*Gadus virens* L.
Hake	*Merluccius merluccius* (L.)
Ling	*Molva molva* (L.)
Argentine	*Argentina sphyraena* L.
Gurnard	*Trigla gurnardus* L.
Angler	*Lophius piscatorius* L.
Conger	*Conger conger* (L.)
Mackerel	*Scomber scombrus* L.
Plaice	*Pleuronectes platessa* L.
Witch	*Glyptocephalus cynoglossus* (L.)
Lemon Sole	*Microstomus kitt* (Walbaum)
Common Dab	*Limanda limanda* (L.)
Long Rough Dab	*Hippoglossoides platessoides* (Fabr.)
Spurdog	*Squalus acanthias* L.
Nurse Hound	*Scyliorhinus canicula* (L.)
Thornback Ray	*Raja clavata* L.
Cuckoo Ray	*Raja naevus* Müller and Henle
Spotted Ray	*Raja montagui* Fowler

Table 17

Mean wind speeds in knots from one hour before to one hour after noon and midnight on the dates when experimental trawl hauls were made

	Series A			Series B
	Noon	Midnight		Noon
25. Aug. 1952	7	?	29. Oct. 1956	14
1. Sept. 1952	18	16	30. Oct. 1956	8
27. Apr. 1953	20	13	31. Oct. 1956	15
4. May 1953	1	0	1. Nov. 1956	0
31. Oct. 1957	22	30	2. Nov. 1956	0

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An Analysis of the Method of Sampling the East Anglian Herring Catches

By

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I. Introduction

Hodgson (1939) described the method by which the catches of the East Anglian fishery were sampled for age. Length measurements were made daily in curing yards, kippering houses, or from the premises of the exporters of fresh herring at both Lowestoft and Yarmouth. These measurements were raised to a weekly age composition by means of an age/length key. A sample of scales from 100 fish, two scales per fish, was taken from a box of herring for this purpose. Four scale samples were taken each week.

On resumption of the sampling programme after the war, measurements were obtained from the same sources as far was practicable; but, with the reduction in the quantities going to the curers and kipper houses increasing numbers of measurements were obtained on the market, particularly at Yarmouth.

In the 1955 season it was decided to put the whole sampling system under review. For convenience, the measuring was concentrated at Lowestoft on the fish market and in the kippering houses. In measuring on the fish market, particular attention was paid to obtaining measurements from as many distinct areas of fishing as possible, e.g., north of Smith's Knoll and south of Smith's Knoll, and also from both English and Scottish vessels in the same area. When possible, two $\frac{1}{6}$ cran boxes of herring were measured from each vessel.

II. Results

A. The kippering yards

In the kippering yards a box containing a known quantity of herring was measured; in some cases this would be $\frac{1}{6}$ cran and in others $\frac{1}{4}$ cran. One box was used as a unit for measuring, as it was found unreliable to sub-sample from a box (Burd and Gulland, 1955).

The measurements made during the 1953 season, which were all obtained from kipper yards at Lowestoft and Yarmouth, were analysed to estimate the "Within Kipper Yard" variance. During this year, in each kipper yard two quarter cran boxes were measured. An analysis of variance on the means of the length measurements in each box appears in Table 1.

Table 1

Analysis of variance of means of measurements from two boxes

(a) *Lowestoft*

Source	Sum of squares	d.f.	Mean square
Within Kipper Yard	0·114	26	0·004
Between Kipper Yards	12·392	38	0·326
Between Weeks.....	11·594	5	2·319
Total	24·099	69	

(b) *Yarmouth*

Source	Sum of squares	d.f.	Mean square
Within Kipper Yard.....	0·034	41	0·001
Between Kipper Yards.....	16·828	38	0·443
Between Weeks.....	21·656	5	4·331
Total	38·517	84	

The "Within Kipper Yard" mean squares are very small, in fact as small as can be expected as the fish in any one sample are not all the same size. Typically a sample contains fish from 22 to 30 cm with a variance of 2·2 cm^2; the expected variance of the mean length of a sample of say 300 fish is therefore 0·007. This agrees well with the values of 0·004 and 0·001 for the "Within Kipper Yard" mean squares. Each kipper yard contains a uniform set of fish.

There is no difference in the "Between Kipper Yards" values at Lowestoft and Yarmouth and the differences between Lowestoft and Yarmouth for the "Between Weeks" mean squares are also insignificant.

At any one time of day it is likely that the fish available for measuring at a kipper yard have come from only one or two boats. By enquiry it is sometimes possible to measure samples from these different sources. In the 1955 season, if no information could be obtained as to source of supply then only one box was measured. The measurer then went to another yard. He could later return to the first yard, where the original supply of fish had been processed, and often obtain a further series of measurements of fish from another source. In this way it was hoped to obtain the maximum amount of information on the variability of the length composition within one kipper yard.

B. The 1955 length measurements

1. Daily measurements. Mean lengths were calculated for each length distribution obtained in the kipper yards and were grouped by the firm of kipperers at which the measurements had been made. An analysis of variance was performed on these means for "Within" and "Between Kipper Yards". The results are given in Table 2. The period during which measurements were made was from 10. October to 19. November.

Table 2

Analysis of variance of means of daily kipper yard measurements

Source	Sum of squares	d.f.	Mean square
Within Kipper Yards.....	1·479	35	0·042
Between Kipper Yards.....	5·966	20	0·298
Between Days.....	69·795	21	3·324
Total	77·240	76	

From Table 2 it is easily seen that by far the greatest source of variance in comparing the means of the measurements is that due to the differences in date of the samples. This is only as may be expected as during the fishing season the young fish mainly arrive first and the older later on. Comparing the mean squares of the "Within" and "Between Kipper Yard" means ($F = 7{\cdot}1$; $p < {\cdot}001$) it is seen that the "Between Kipper Yard" mean square is significantly greater than that "Within Kipper Yards".

Comparing the values of the "Within Kipper Yards" mean squares of 1953 and 1955, it is seen that the value for the latter year is much greater than the former; due doubtless to the deliberate prevention in 1955 of replication from one source, as described above.

Taking the same period, 10. October to 19. November, an analysis of variance was performed on the means of the individual measurements made from ships' catches on the quay. In this analysis no attention was paid to any differences between Scottish and English vessels or to differences in fishing areas. The results of the analysis of variance appear in Table 3. The "Within Ship" variance is an estimate of the differences in mean lengths between replicate samples from one ship.

Table 3

Analysis of variance of means of market measurements

Source	Sum of squares	d.f.	Mean square
Within Ships	3·705	63	0·059
Between Ships	57·437	112	0·513
Between Days	175·961	26	6·768
Total	237·103	201	

Again it is seen that the largest component of variance is that due to date of sampling. Comparing the mean squares of the "Within" and "Between Ships" means ($F = 8{\cdot}7$; $p < {\cdot}001$) it is clearly seen that the differences in means between ships is vastly greater than the differences between boxes in the catch of one vessel. One box taken at random from the catch of a drifter should therefore be an adequate sample of the vessel's catch.

Comparing the "Between Days" mean squares of the kipper house and market means there is no significant difference in their values. The values obtained for the "Within Source" variances are also not significantly different. This would imply that the variation of the means of multiple measurements made in one kipper yard are of the same order as the differences between boxes in the catch of a single ship. This would arise in the kipper yards if a selection took place in buying fish, and if the kipper yard sample did indeed tend to be the catch of a single ship.

However, comparing the "Between Kipper Yard" measurements with those from "Between Ships" there is less variance between the former than the latter ($F = 1{\cdot}7$; $p > {\cdot}05$). In other words the differences between measurements from different kipper yards is less than that found between the measurements from different ships on the market. In fact, if means of all measurements from both places, kipper yards and market, are taken daily it was seen that in 1955 the mean lengths obtained from the kipper yards were generally bigger than those obtained on the fish market (Fig. 1, Table 4). When the *t*-test was applied to

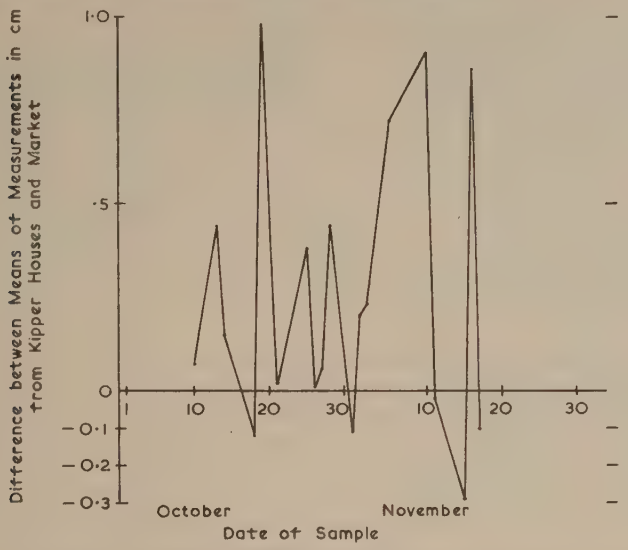

Figure 1. 1955 daily measurements. Differences between the daily means of measurements from the kipper yards and the fish market during the season.

the differences between the means of the kipper house measurements and the market measurements, these were found to be highly significantly different. There was a mean difference of 0·24 cm.

A second feature which is apparent on inspection of Table 4 is the change in mean length through the season. It is this variation which is estimated in the "Between Days" variance in the previous analyses.

Two explanations can be suggested for the difference between measurements from the two sources. Firstly, the merchants who buy for kippering may deliberately buy the largest fish that are landed. The second explanation might be that because of their need for early supplies the kipperers tend to buy from, say, the first vessels to arrive which may have been fishing in a particular

Table 4

Daily mean lengths in cm from kipper yard and market

Date	Kipper yard	Market	Date	Kipper yard	Market
10. October	24·70	24·63	1. November	25·86	25·97
13. –	25·33	24·89	2. –	26·97	26·77
14. –	25·11	24·96	3. –	26·88	26·65
18. –	24·63	24·85	5. –	27·01	26·29
19. –	25·56	24·66	10. –	27·14	26·24
21. –	25·58	25·60	11. –	26·80	26·82
25. –	25·27	24·89	15. –	26·35	26·64
26. –	24·39	24·40	16. –	27·37	26·51
27. –	24·40	24·34	17. –	26·18	26·28
28. –	25·72	25·28			

area. It was decided to analyse the data again on a 3-day period basis to see if any of these explanations might be applicable.

2. Three-day periods. Taking the same period of time as in the previous section an analysis of variance was performed on all kipper yard measurements irrespective of source. The results appear in Table 5.

Table 5

Analysis of variance of mean lengths of fish from kipper yards

Source	Sum of squares	d.f.	Mean square
Between Samples	16·048	65	0·247
Between Periods	61·192	11	5·563
Total	77·240	76	

As would be expected the "Between Samples" mean square approaches that of the daily "Between Kipper Yards" value in Table 2.

In dealing with the data from the fish quay if more than one box had been measured from a ship then a grand mean was calculated for that ship. Where measurements were taken from one ship on more than one occasion of landing during the 3-day period, each daily measurement has been regarded as if landed by a different ship. The results of the analysis appear in Table 6.

Table 6

Analysis of variance of 3-day period mean lengths

Source	Sum of squares	d.f.	Mean square
Between Landings	45·905	127	0·361
Between Periods	99·276	11	9.025
Total	145·181	138	

Though the "Between Periods" mean square in this case is greater than that for the kipper yards they are not significantly different. Again the "Between Landings" mean square approaches the daily "Between Ships" value.

The "Between Landings" variance is made up of a number of components, those due to position of fishing (area) and those due to nationality because English and Scottish ships use slightly different sizes of nets. The area of the East Anglian fishery is subdivided for statistical purposes into small squares 10 minutes of longitude by 10 minutes of latitude as shown in Figure 2. At any time the drifter fleet is usually distributed narrowly east and west but over a large distance north and south. In this analysis the length measurements have been grouped into north-south areas, G-K, LMN, OP, QR, and S. Results of the analysis of variance are shown in Table 7.

Table 7

Analysis of variance of 3-day period mean lengths

Source	Sum of squares	d.f.	Mean square
Within Areas.....	16·415	106	0·155
Between Areas	29·490	21	1·404
Between Periods	99·276	11	9·025
Total	145·181	138	

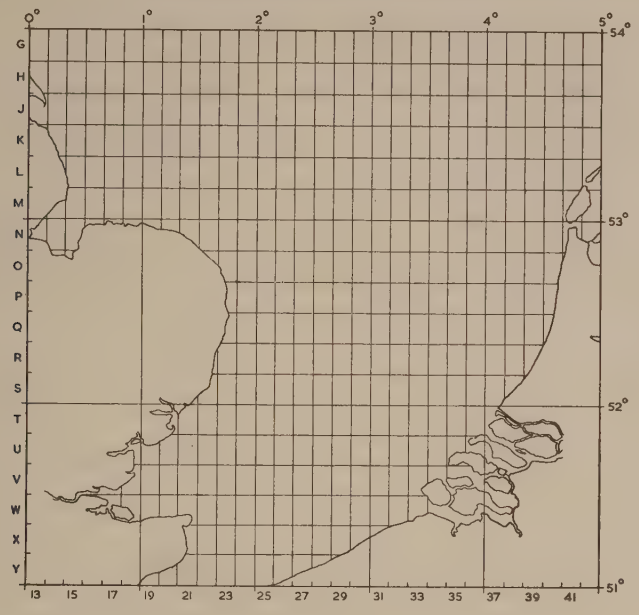

Figure 2. Statistical rectangles used in the East Anglian fishery.

From this analysis it is evident that by far the largest source of variation at any time is that caused by area of fishing; the variance between means within an area are comparatively negligible. In Table 8 the values of the mean squares by 3-day periods are presented.

These are plotted in Figure 3, where it is seen that, while the "Within Area" mean squares vary little with time, those for the "Between Areas" vary considerably, becoming less during November. In other words there is a greater

Table 8

Mean squares and degrees of freedom for 3-day period means of measurements from kipper houses and market by areas

Date	Kipper Yards Samples Mean sq.	d.f.	Between Areas Mean sq.	d.f.	Within Areas Mean sq.	d.f.
10.–12. October ..	0·07	6	0·00	1	0·08	6
13.–15. – ..	0·06	7	0·17	2	0·05	22
17.–19. – ..	0·71	5	2·29	2	0·07	10
20.–22. – ..	0·06	3	1·96	1	0·17	2
24.–26. – ..	0·27	9	1·85	2	0·20	8
27.–29. – ..	0·68	7	4·91	1	0·21	10
31.– 2. November	0·31	7	1·96	2	0·23	12
3.– 5. –	0·08	9	0·77	2	0·17	10
7.– 9. –	0·00	1	2·31	2	0·13	1
10.–12. –	0·04	5	0·87	3	0·22	11
14.–16. –	0·35	3	0·57	2	0·24	12
17.–19. –	0·04	3	0·16	1	0·02	2

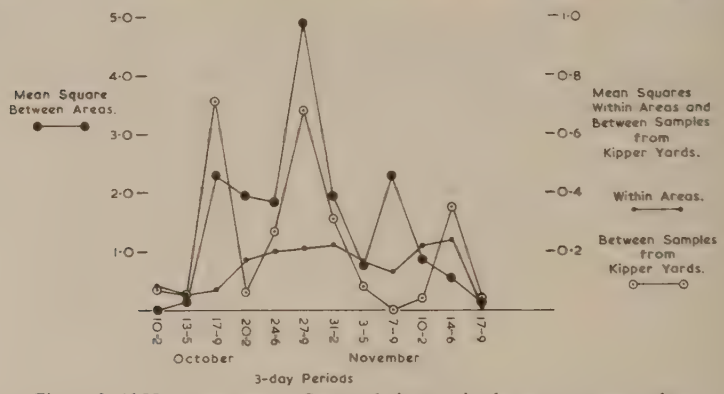

Figure 3. 1955 measurements. Seasonal changes in the mean square values.

difference between the length distributions north-south in October than November. Owing to the growth pattern of the herring, there are only relatively small changes in the mean lengths of 6 to 9 year-old fish compared with those changes in the means of 3 to 5 year-old fish. As November is the season for old fish to appear in the catches one would expect less difference in the mean lengths of samples taken by areas in this month, as has been shown in the analysis of variance.

In value, the mean squares from the kipper house measurements are closer to the "Within Area" values than those for "Between Areas", but they show in part similar fluctuations to that for "Between Areas".

Taking the areas LMN, OP, QR, and S, for which most data are available and from which about 90% of the total catch was obtained, the deviation of the individual means for an area from the grand mean of the 3-day period concerned have been plotted in Figure 4. From this it is clearly seen that, taking the season as a whole, there are larger fish in the north than in the south.

In the same manner, but using weekly periods instead of 3-day periods, the relation between area means, east and west, was tested. From Figure 5, it can be seen that there is a tendency for larger fish at any time to be those further to the east. The bias in the measurements from the kipper yards could then arise either by the merchants actually buying the largest fish they could see or by their consistently buying from a northern area. It would seem unlikely in this case that the differences in mean lengths between the measurements from the kipper yards and market could be arrived at by chance.

There still remains the question of how much the "Between" and "Within Area" difference might be caused by the relative distributions of English and Scots vessels. It was therefore necessary to compare the variances between English and Scottish vessels with that "Between Areas". If the "Between Area" variance was caused solely by the differences in distributions of the various vessels by nationality then the mean squares of the two nationalities "Within Areas" should be similar to the "Between Area" mean square. Using only the observations where both English and Scots measurements from the same square had been obtained, Table 9 gives a summary of the data by nationality by 3-day periods.

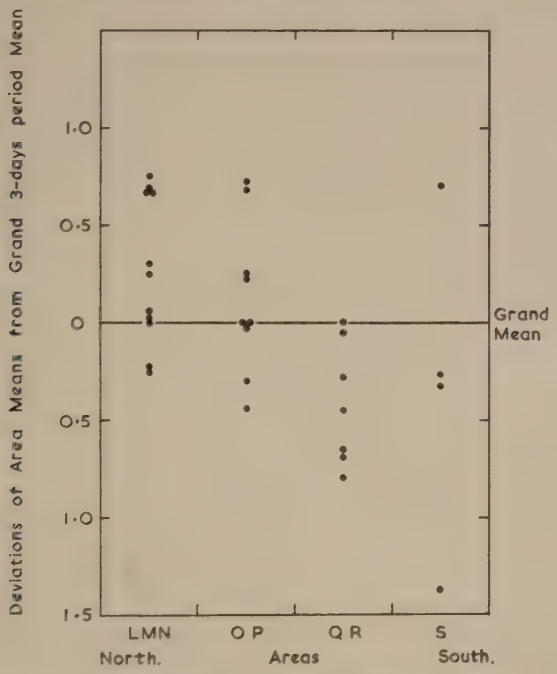

Figure 4. 1955 measurements. North/south distribution of mean lengths during the season.

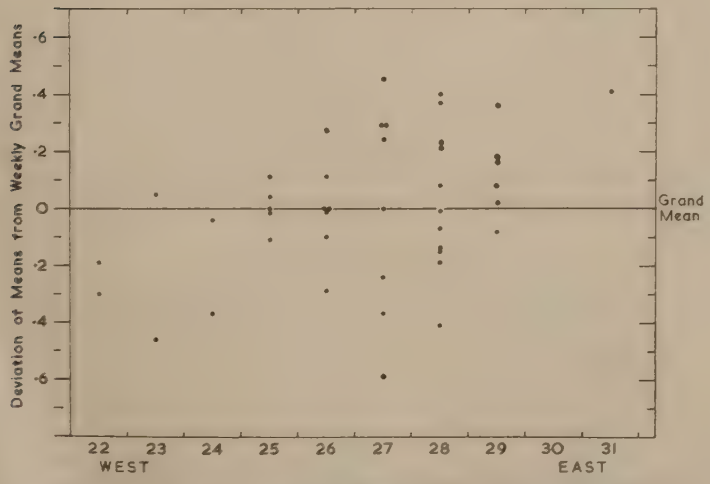

Figure 5. 1955 measurements. East/west distribution of mean lengths during the season.

Table 9

Analysis of variance of market measurements by nationalities

Date	A Between English Sum of squares	d.f.	B Between Scots Sum of squares	d.f.	C Between English & Scots Sum of squares	d.f.	A + B + C Within Areas Sum of squares	d.f.
10.–12. October	0·423	5	–	–	0·061	1	0·484	6
13.–15. –	0·346	10	0·414	10	0·404	2	1·164	22
17.–19. –	0·082	4	0·596	5	0·051	1	0·730	10
20.–22. –	0·185	1	0·157	1	–	–	0·342	2
24.–26. –	0·899	6	–	–	0·693	2	1·592	8
27.–29. –	1·888	3	0·132	5	0·118	2	2·138	10
31.– 2. November	1·176	6	0·426	4	1·148	2	2·750	12
3.– 5. –	1·641	9	–	–	0·011	1	1·652	10
10.–12. –	1·252	10	–	–	1·217	1	2·469	11
14.–16. –	2·928	11	–	–	0·004	1	2·932	12
17.–19. –			0·024	1	0·008	1	0·032	2
Total	10·820	65	1·749	26	3·716	14	16·285	105
Mean square	0·17		0·07		0·27		0·16	

	Sum of squares	d.f.	Mean square
Between Areas (from Table 8)	24·869	19	1·31

Comparing the mean square of "Between English and Scots" with that "Between Areas" it is found that the latter is significantly different from the former, ($F = 4{\cdot}85$; $\cdot 01 > p > \cdot 001$). Thus the differences between areas could not be ascribed solely to the differences in distribution of the Scots and English drifters.

C. The 1953 and 1954 length measurements

Prior to 1955 the sampling was not designed to test the differences which have become apparent in the above analyses. However, the data from previous years afford some further information on the sampling problem.

The analysis of variance of the measurements in 1953 have already been commented upon, in that they demonstrate the small variance of replicate samples in a kipper yard. In addition, 1953 affords a complete comparison of data obtained at both ports. In Table 10, the analysis of variance of all kipper yard measurements are shown for Lowestoft and Yarmouth, together with a residual.

Table 10

Analysis of variance of 1953 kipper yard length measurements

Source	Sum of squares	d.f.	Mean square
Within Lowestoft	24·099	69	0·35
Within Yarmouth	38·517	84	0·46
Residual (between ports)	2·054	1	2·05
Total	64·670	154	

Comparing the Lowestoft and Yarmouth mean squares ($F = 1{\cdot}3$) it is seen there is no significant difference in the variance. However, the high residual,

Table 11

Analysis of variance of 1954 market measurements

Source	Sum of squares	d.f.	Mean square
Between Ships, Lowestoft . .	6·873	30	0·229
Between Ships, Yarmouth. .	11·744	72	0·163
Between Lowestoft and Yarmouth	2·287	4	0·572
Between Weeks	17·711	3	5·904
Total	38·614	109	

Table 12

1954 grand weekly means

Week ending	Lowestoft	Yarmouth
9. October	25·30	25·10
16. –	24·99	24·83
23. –	25·78	25·59
30. –	26·14	25·61

"Between Ports" mean square indicates there is a significant difference between the two ports. Taking the season as a whole, the grand mean length for Lowestoft was 25·27 cm and for Yarmouth 25·50 cm. Thus Yarmouth had significantly bigger fish than Lowestoft.

During 1953 very few measurements were made on the market. The numbers are too few to afford any estimate of the possible bias due to the use of measurements from the kipper yards.

The 1954 measurements at Yarmouth were made on the quay, while at Lowestoft some were taken both at kipper yards and on the quay. Only one box of fish was measured from any one ship or kipper yard. The measurements, therefore, afford a comparison between the ships at the two ports. For October means were calculated and an analysis of variance was performed on these, which is summarized in Table 11.

From this it is seen that there is a significant difference between vessels at Lowestoft and Yarmouth. The variance "Between Ships" in each port is similar.

The grand weekly means of ships measurements at Lowestoft and Yarmouth in 1954 are given in Table 12.

In this year the grand mean of the Lowestoft measurements was 0·38 cm larger than that from the Yarmouth ships. This is in contrast with 1953 when they were smaller.

From the data it is clearly seen that the variances estimated at each port are similar. However, there may be a consistent difference in the mean lengths at each port. This may be due to the fact that the Scots tend to go to Yarmouth, while at Lowestoft there are both Scots and English.

D. The age distributions

Referring again to Table 4 the bias in the measurements from the kipper yards will affect the age distributions for the year. In 1955 two methods were used for taking scale samples for construction of the age/length key. In the first method 100 fish were scaled from a box of herring, the fish being taken at

Table 13

Average number per landing at Lowestoft in thousands at each age

Week ending:		Age in years 2	3	4	5	6	7	8	9	10	10+
15. Oct.	Hodgson key	0·1	11·8	7·6	2·1	0·4	0·3	0·2	–	–	0·0
	Selected key .	0·1	12·1	7·4	2·2	0·4	0·2	0·1	–	–	0·0
22. Oct.	Hodgson key	–	13·0	9·6	3·5	1·4	0·4	0·3	0·1	–	–
	Selected key .	–	11·8	10·3	3·8	0·9	0·1	1·0	0·1	–	–
29. Oct.	Hodgson key	–	19·3	9·8	3·0	0·9	0·1	0·5	0·1	0·0	–
	Selected key .	–	19·4	9·6	2·9	1·0	0·2	0·3	0·2	0·0	–
5. Nov.	Hodgson key	–	4·0	7·6	6·7	4·1	1·6	1·4	0·9	0·3	0·5
	Selected key .	–	4·6	6·5	6·3	4·8	1·9	0·9	1·0	0·7	0·4
12. Nov.	Hodgson key	–	3·7	7·5	8·2	5·0	1·6	1·2	1·6	0·8	0·7
	Selected key .	–	4·2	7·9	6·6	5·0	2·2	1·8	1·6	0·8	0·2
19. Nov.	Hodgson key	–	6·4	6·5	5·8	4·8	1·8	1·3	1·0	0·7	0·6
	Selected key .	–	7·0	5·6	6·3	4·6	1·7	1·6	1·2	0·5	0·5

random. About 2,400 fish were used in the construction of the key. This was the method employed by HODGSON. In the second method 10 or more fish were collected from a number of vessels on the market, so that every major area was sampled from both English and Scottish vessels. The various samples of 10 fish were kept separate. If possible equal numbers of fish at each centimetre class were selected for scale taking from these samples. About 3,000 fish were examined for age in this method.

Using the two age/length keys, the measurements from the kipper yards were raised. In Table 13 the average number per landing in thousands of fish are shown by weeks, calculated by the two methods. There is no significant difference in the age distributions calculated by the two keys.

Using the selected sample age/length key, the length measurements obtained from herring in the kipper yards and on the market were raised separately. Table 14 shows the number of fish per landing at Lowestoft and Yarmouth for each week of the 1955 season.

Taking the season as a whole there was an underestimate of the numbers of 3-year-olds by kipper yard measurements of about 16%. There were about

Table 14

Average number per landing at Lowestoft and Yarmouth in thousands at each age

Week ending	Source	Age in years 2	3	4	5	6	7	8	9	10	10+
15. Oct.	Kipper House	·06	12·11	7·36	2·25	·44	·19	·11	–	·02	·04
	Market.....	·06	13·49	7·02	1·95	·29	·13	·06	–	·01	·02
22. Oct.	Kipper House	–	11·80	10·28	3·83	·88	·08	1·02	·06	–	–
	Market.....	–	16·59	8·55	3·01	·77	·13	·21	·09	–	–
29. Oct.	Kipper House	–	19·45	9·64	2·91	1·00	·18	·28	·21	–	–
	Market.....	–	21·14	9·14	2·59	·87	·10	·22	·13	–	–
5. Nov.	Kipper House	–	4·63	6·52	6·31	4·77	1·87	·87	1·01	·66	·45
	Market.....	–	6·48	6·95	5·74	4·28	1·69	·80	·91	·61	·41
12. Nov.	Kipper House	–	4·22	7·93	6·55	5·01	2·25	1·84	1·61	·77	·22
	Market.....	–	5·70	8·40	5·87	4·63	2·09	1·74	1·53	·72	·22
19. Nov.	Kipper House	–	7·04	5·59	6·29	4·55	1·72	1·60	1·18	·49	·51
	Market.....	–	7·36	5·61	6·20	4·47	1·70	1·61	1·15	·49	·50

Table 15

Weighted area variances, $\sigma^2_{\bar{x}}$, and respective mean length and total catches

Date	$\sigma^2_{\bar{x}}$	Mean length, cm	Catch (crans)
10.–12. October.....	0·0013	24·74	1096
13.–15. –	0·0020	24·91	2754
17.–19. –	0·0058	24·89	3509
20.–22. –	0·1005	25·04	682
24.–26. –	0·0129	25·00	6896
27.–29. –	0·0662	24·54	8276
31.– 2. November	0·0154	26·35	9223
3.– 5. –	0·0124	26·54	5163
7.– 9. –	0·3694	25·90	4929
10.–12. –	0·0105	26·59	7137
14.–16. –	0·0210	26·74	8066
17.–19. –	0·0118	26·26	4200

3% more fish of 4 and about 10% more fish of 5 years old in the measurements from the kipper houses. The differences in the older age-groups are insignificant. Using the *t*-test the deviations of the 3, 5, and 6 years old fish are significant at the 95% level.

The largest component of variance extracted in the above analyses of the market measurements was seen to be that due to differences in the areas in which the vessels were fishing. However, in this calculation no account had been taken of the catch distribution over the areas. Any box taken on the market at random would be likely to come from the catch of a vessel from one of the more heavily fished areas than from a lightly fished area. In order to estimate the confidence limits for a single observation it is therefore necessary to use the variances of the area means weighted by their respective catches.

These weighted variances are shown in Table 15 calculated on a 3-day period basis, and also the corresponding grand means of measured samples and the total catches are given. An example of the method of calculation of the variance of the weighted area means is given below: —

	Area	Catch (crans)	Mean sq.	Observations (samples)
17.–19. October	LMN	1066	·0133	4
	OP	400	·0421	2
	QR	2043	·1079	7

$$\text{Variance of Area Means} = \sigma^2_{\bar{x}} = \frac{\frac{\cdot0133 \times 1066^2}{4} + \frac{\cdot0421 \times 400^2}{2} + \frac{\cdot1079 \times 2043^2}{7}}{(1066 + 400 + 2043)^2}$$

$$\sigma^2_{\bar{x}} = \cdot0058$$

The grand seasonal mean, weighted by catches, is

$$\frac{24{\cdot}74 \times 1096 + 24{\cdot}91 \times 2754 + \ldots\ldots\ldots 26{\cdot}26 \times 4200}{1096 + 2754 + \ldots\ldots\ldots 4200} = 25{\cdot}81 \text{ cm.}$$

The variance of the weighted area mean for 7.–9. November is high. Only four samples were measured during this period and their means are shown below: —

Area	Mean length, cm	Catch (crans)
LMN	27·27	2935
OP	—	1732
QR	—	30
S	26·62	190
Gabbards	25·10 24·59	42

The difference of nearly 3 cm in the means results in a high "Between Area" variance. As can be seen most of the measurements came from the most southern areas where the catches were small.

In calculating the variance of the area means, weighted by catch, one assumes in this case that the variance of the mean lengths of samples within the high catch areas of the north is the same as that calculated for between areas, i.e., LMN, S, and Gabbards. As has been shown previously the northern areas at any one time usually have the larger fish. The variance calculated is thus biased by the north/south distribution of the fish, which can be seen in Figure 4.

In calculating the mean variance and the weighted areas mean the observations for this period have been omitted. Their values appear below: —

$$\text{Mean } \sigma^2_{\bar{x}} = 0{\cdot}0236$$

$$\text{Grand weighted area mean} = 25{\cdot}81 \text{ cm.}$$

$$\sigma_{\bar{x}} = 0{\cdot}154$$

The 95% confidence limits for the grand mean are then: —

$$25{\cdot}81 \pm \sigma_{\bar{x}} \times 1{\cdot}96 = 25{\cdot}81 \pm 0{\cdot}30$$

Thus the mean length of all herring landed lies between 25·51 and 26·11 cm. Using this information it is possible to estimate the error on the estimated numbers of fish in an age-group. If p_1 is the proportion of fish in an age-group and $\bar{x}_1$ its mean, and $(1 \quad p_1)$ is the proportion of fish in all other age-groups and $\bar{x}_2$ is its mean; then, if $\bar{x}_1$ and $\bar{x}_2$ are known, p_1 may be determined from the formula

$$25{\cdot}81 = \text{grand mean} = p_1 \bar{x}_1 + (1 - p_1)\, \bar{x}_2$$

This formula is only reliable when $\bar{x}_1$, is very different from $\bar{x}_2$. The most reliable estimate of the numbers in any particular age-group will be that for the 3-year-olds — which are also the most abundant of the age-groups. The calculations appear below: —

$$\text{Grand Mean} = p' \times 23{\cdot}96 + (1 - p')\, 26{\cdot}68$$

$$p' = 32{\cdot}0\%$$

At the upper confidence limit of the grand mean (26·11)

$$p'' = 21{\cdot}0\%$$

and at the lower confidence limit of the grand mean (25·51)

$$p''' = 43{\cdot}0\%$$

Thus the error in the annual estimate of the 3-year-olds in 1955 due to area differences was ± 11%. Because the method above is not the most sensitive test of the variance of the numbers of 3-year-olds, the limits above for the number of 3's landed are probably too wide.

III. Discussion

The analyses of the 1955 data have shown clearly that the use of measurements from kipper yards gives a biased estimate of the population means. This bias leads to an underestimate of 16%, in this case, in the numbers of recruits landed. Unfortunately no reliable comparisons for other years are available. If this is indeed a regular feature, then in the years when only kipper yard measurements were made there is a possibility that the numbers of recruits landed have been underestimated and that the older fish in the catches have been correspondingly slightly overestimated.

Comparing the values of the "Between Ships" mean square of 1954 (Table 11) at Lowestoft with that of the "Between Landings" of 1955 (Table 6) they are not significantly different. The methods of sampling in the two years are therefore quite comparable. Thus the 1954 age distribution is likely to be a better estimate of the true age distribution than those of the previous years which were based on kipper house measurements.

From the analyses of the 1953 and 1954 data it has been shown that there can be significant differences between the mean lengths of the herring landed at Lowestoft and at Yarmouth. The differences in the two years under review were not of the same order. However, no significance can be allotted to this observation as in one case the measurements came from the market and in the other from kipper yards. In both cases the variances between the individual measurements in each port were similar. The changes which occur throughout the season are therefore equally well estimated by using data from either one or other of the ports.

Taking the 1955 market data it was shown that the variance "Within Ships" catches was very small and that the most important variance was "Between Ships". This "Between Ship" variance measures the differences caused by the area in which the vessel fished and also other factors such as size of mesh in the nets.

The data were further analysed to demonstrate any differences in the length composition between areas. The following were the mean squares extracted: —

Between Areas	1·404
Within Areas	0·155

The "Within Area" variance was further divided by catches of English and Scottish vessels and their variances estimated. The mean squares extracted were: —

Between English Ships	0·17
Between Scots Ships	0·07
Residual (Between English & Scots)	0·27

These "Between Ship" variances contain a component of variance due to sampling within the catch of one vessel and also components of variance due

to other sources the most important of which is undoubtedly that due to differences in selection due to mesh size. However, these differences in the means of English and Scottish vessels are not great enough to account for the differences found "Between Areas" even if all the Scots and all the English fished in separate areas. Over the season the largest fish are taken in the north and east.

Using measurements from the fish market, the greatest source of error in estimating the age composition of the catches would therefore be that due to indiscriminate sampling of the fishing areas. Using the "Between Area" variance, the 95% confidence limits of the grand seasonal mean were calculated. These were 25·51 and 26·11 cm, the grand seasonal weighted mean being 25·81 cm.

Using these limits it was calculated that the corresponding error due to area of sampling on the average number of 3-year-old fish in the catch was $\pm$ 11%.

IV. Summary

1. During the 1955 season, it was shown that the mean lengths of fish measured in the kipper yards were consistently bigger than those from the fish market.

2. This would have resulted in an underestimate in the numbers of 3-year-olds in the catches of 16%, if the kipper yard measurements were used.

3. From the market measurements it was shown that the larger fish tend to be in the north and east of the fishing areas.

4. At any one time, the greatest source of variance in the mean lengths of samples is due to this area difference.

5. The error on the estimated average number of 3-year-old fish per landing due to the area of sampling was $\pm$11%.

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Estimation of the Stock Strength of the Norwegian Herring

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I. Introduction

The present paper deals quantitatively with the recaptures from the Norwegian-Icelandic herring tagging experiments in the 5-year period 1950–1954. In the first part of the paper are expounded some theoretical considerations while in the second part the results are discussed giving the first attempt to arrive at an estimate in absolute figures with respect to the numerical strength of the Atlanto-Scandian herring stock.

I am greatly indebted to Dr. Árni Friðriksson for kindly placing at my disposal the data obtained from the Icelandic herring taggings.

II. Theory

The idea of employing the recaptures from taggings in estimation of the stock strength, is founded on the assumption *that tagged and untagged fish are caught in the same proportion.* In mathematical terms we may express our assumption in the following way:

$$\frac{y}{S} = \frac{R}{t} \tag{1}$$

where y denotes the fishery yield,
S the stock present,
R number of recaught tagged fish, and
t the tagged fish present.

In principle the calculation of the stock strength is very simple. For various reasons, however, the practical task is more complicated. A necessary condition for the validity of our basic assumption is that the tagged fish are evenly distributed in the stock, or that the fishing fleet is randomly distributed. Also it is required that they are sufficiently numerous to appear in representative numbers in the catch. From this follows firstly, that we must allow for a certain

time after tagging before the spreading can be effected, and secondly that the number of liberated tagged fish must be in relation to the suspected fishing mortality. It must be left to a consideration of the actual recoveries to decide whether these basic requirements are satisfied reasonably well for practical purposes. But even if we knew this to be the case, the calculation of the stock would still not be a straightforward task. The figures y, R, and t are not known and have to be derived from the catch statistics, recovered tags, and tagged amounts respectively. We might express this for short:

$$y = f(c) \tag{2}$$
$$R = \varphi(r) \tag{3}$$
$$t = \psi(T) \tag{4}$$

where c is the landing figure,
r the recovered tags, and
T the tagged amount.

Before the stock calculation can be carried out, we must establish these relationships. We will consider the functions in turn.

$y = f(c)$. The form of this equation is dependent on the unit in which we choose to express our stock figure. In Norway, the landing figure, c, is usually given in hl, which is the original measuring unit when the fishermen bring in their catches for delivery. Owing to the rather unique fishermen's sales organization, in which all catches are recorded, the statistics, c, is brought to a very high standard of accuracy. We may therefore place confidence in this figure, the error of which is probably only a fraction of one per mille and ought not to influence the result unduly. If we want to have our stock figure expressed in hl, equation (2) takes the simple form $y = c$ and this will be sufficient in most cases. For some purposes, however, it is desirable to have the catch expressed in number of individuals. The figure, c, must then be converted by means of sampling data. This can be done in various ways. In any case it will be a formidable task if accuracy is required. With a proper knowledge of the average number of herring per hl equation (2) would take the form: $y = \bar{a} \times c$, where $\bar{a}$ denotes the average number of individuals per hl. The first approximation to $\bar{a}$ is obtained by averaging all the samples. A better estimate is effected by breaking down the catch statistics into "area-time" cells and weighting the samples. How far this breaking can be carried, will depend on the number and distribution of the samples and on the structure of the statistical system. In Norway, we will have to be contended with pooling the samples within each week and weighting them by the weekly landings. If the average number of herring per hl within each week is denoted by a', a'', ..., $a^{(n)}$ and the weekly landings by c', c'', ..., $c^{(n)}$, we get:

$$y = a' \times c' + a'' \times c'' + \ldots + a^{(n)} \times c^{(n)}$$

Naturally we cannot be fully confident in the figure y in this case. A rough calculation shows that there will be about half a million times more herring in the catch than those covered by the sampling in the later years. Moreover, the samples are almost exclusively based on seine-caught herring because the gill-nets act selectively. This will in turn bias the result since the gill-nets are responsible for a substantial portion of the catch.

$R = \varphi(r)$. In our tagging experiments we have mainly been using internal steel tags as will be evident from this and earlier reports from the taggings

(Friðriksson and Aasen, 1950, 1952). In the estimation of the stock the results from the internal taggings only will be considered.

To the actual number of tags returned to the proper authorities, we may allow for a certain number of tags lost after recovery. This problem, however, is greatly simplified by the fact that the overwhelming majority of the returns come from the magnetic separators which have been installed in the reduction plants. In the factories there are only a few workers who attend to that part of the machinery where the magnets are placed, and thus we have only to deal with a fairly limited number of people. In all the plants there are placed posters with detailed instructions of what to do with the recovered tags. The object and importance of the tagging experiments are explained, and in order to further stimulate the interest a worthwhile reward is offered for each recovery. This last is not the least important in carrying the tagging scheme with due respect to the genuine interest on the part of the managements and employees of the reduction plants. The premium paid is evidently so tempting that it is reasonable to suppose that the finder will try to get his money. In some few cases there have been reports on losses of tags after recovery. In such cases no reward is paid unless the numbers are noted and the actual finding is certified by reliable witnesses. Such reports run about one per mille of the total returns and may be regarded as insignificant. In a couple of instances false tags have been forwarded. They are easily spotted and no reward is paid. Their number is quite negligible. Tags may also be rendered unreadable in the machinery. For such tags the premium is paid to encourage reports of this kind. The number of unreadable tags is about three per mille of the total, and may be disregarded. That tags should be kept for souvenirs is not very likely since herring tags are now a quite familiar object in the factories, and it is likewise not probable that a significant number of recoveries should fail to be forwarded through neglect. As a whole we may be justified in disregarding losses of tags after recovery in the reduction plants. Without doubt the small error thus introduced will be completely overshadowed by the error arising from another source presently to be dealt with. As well known, only a part of the catch is reduced to oil and meal. We may well assume that there will be proportionately the same amount of tags in the other part used in fresh, frozen, or cured condition. It is easy to correct for the number of overlooked recaptures in this part since the factories keep very accurate records of the reduced quantity. The discrepancy emerging from this operation would not amount to much. In the same way we may cut out and correct for the amount going through factories without magnetic separators or with faulty installations. But the question still remains how many tags, going through a plant with satisfactory magnets, will get stuck in the machinery or fail to show up on the separator for other reasons. No doubt there will be a substantial amount of recovered tags disappearing this way. To overcome this difficulty the efficiency of the magnets has been tested by tagging a known number of herring and placing them on the conveyor-belt from the storage bins. The fraction between the recovered tags and the tagged number provides an estimate of the efficiency of the magnet. Such efficiency tests have been carried out in most of the plants, but unfortunately it has not been possible to cover every factory in all years. These tests may sometimes show varying figures from year to year and even within the same season for the same factory in which case we may choose one or the other or taking the average value if the results are fairly close. Obviously, here may be introduced errors

which seriously will affect our calculations. It is a comforting thought that since we operate with many plants the errors will supposedly be on either side of the correct figure and thus in the end be evened out. As a result of the preceding discussion the following expression for equation (3) emerges:

$$R = \frac{r}{e} \times \frac{c}{p}$$

where r is the actual number of returns,
e the efficiency of the magnets,
c the landing figure, and
p quantity reduced in plants

since r, c, and p are precisely known this expression demonstrates clearly the prime importance of e.

$t - \psi(T)$. As soon as a batch of tagged herring is liberated on the fishing ground, things start happening which will reduce the number. When analysing these reductive agents, we might as well start thinking in terms of seasons because both the Icelandic and the Norwegian fisheries for mature herring are typically seasonal.

It is important to know what is left of the tagged fish when the season closes. Any tagging mortality and shedding of tags will presumably take place relatively soon after tagging. It is then possible to investigate empirically whether excessive mortality is induced by the tagging or if any shedding occurs. In report No. 1 on the taggings is referred to some experiments with respect to the vitality of the herring after tagging. The conclusion drawn from these experiments was that the tagging did not affect the herring seriously when properly executed on fish in good condition (FRIÐRIKSSON and AASEN, 1950). The fact that tags are still returned in number after six years[1] in the sea, supports this view. So do also the results from the double taggings, in which both internal and external tags are fitted to the fish. Double tagged herring have been brought in to the Marine Research Institute in Bergen after different lengths of time at liberty. Although the material is scanty for a thorough judgment, it seems that the wound shows signs of healing after a fortnight. It may be visible for a couple of months, but after one year in the sea, the wound is completely healed and not even a scar can be seen. In no case could the internal tag be seen to have done damage to vital organs, but they are frequently found inside the gonads which is quite natural since it is mostly full herring which have been double tagged. Wounds in the gonads are evidently not fatal. The tags show never any signs of corrosion and as a whole we may conclude that internal tags cause no harm which is not healed after comparatively short time. With the evidence from the vitality experiments, supported by the observations on the internal tags in recaught doubly tagged herring, and further corroboration from the returns six years after tagging, it is reasonable to assume that no significant excessive mortality is induced by the tagging.

Parallel with the "live" experiments in 1948 and 1950, there were also carried out shedding tests. The first of these experiments yielded a shedding percentage of 1 % after 14 days. The second experiment showed no shedding of tags after 19 days (FRIÐRIKSSON and AASEN, 1950). According to this, shedding may be

[1]) By later records, ten years.

regarded as insignificant. There is, however, evidence which contradicts this conclusion. In two cases in 1952, the internal tags were reported missing in recaptured double tagged herring. One of these reports came in from Sweden, the other one from Scotland, and these observations leave doubt as to the validity of the earlier conclusion regarding the shedding. These herrings were tagged in the first large scale double tagging experiment and the technique has since then been completely revised by introduction of the "tagging sluice". From the later experiments there are no records of missing internal tags. The question will receive close attention in the future. In the meantime, however, we maintain the first conclusion that no significant shedding takes place with internal taggings when it is carried out properly.

If tagging mortality and shedding are ruled out as insignificant, the only other sources for depletion of the tagged number of fish within the tagging season are natural and fishing mortality. The first of these cannot be evaluated at present, and the other will also offer difficulties. Because of the time lapse necessary for the tagged herring to spread in the stock, we cannot be sure that the tagged fish will be caught in the same proportion as the untagged. The calculation of the probable number of recovered tags within the tagging season is thus rendered difficult. Fortunately, the returns are few. The actual number of returns must be reckoned in per mille, and the error introduced when disregarding them will not seriously affect the result. This is particularly true for the spring herring taggings carried out at the very end of the season. (For one tagging experiment in 1951, 8 B, carried out in inshore waters, the returns were very numerous. This experiment will have to be discarded for the stock calculations).

After the herring has left the fishing grounds, there are two possible ways of accounting for the number not returning the following season. One part will die for some reason. The quotient between the remaining and the original number of tagged herring we will call the coefficient of survival, ϱ. We cannot be sure, however, that all the surviving herring will be present on the fishing grounds in the next season. It has been customary to regard the Norwegian winter herring as a fairly well defined tribe which only to a moderate extent intermixes with the herring tribes in adjacent waters. The taggings have revealed, however, that, in some years at least, substantial numbers migrate into the North Sea and the Skagerak and mix with the herring there (Friðriksson and Aasen, 1952; Aasen, 1953). This observation is not new, for Einar Lea found the same general feature many years ago through his scale studies (Lea, 1930). This "dispersal" has an important bearing on our problem. It may and may not be that the herring spread out in this manner will be lost in the future for the spawning shoals on the Norwegian coast. The taggings have yielded evidence that herring may visit entirely different spawning grounds in different years (Friðriksson and Aasen, 1952). We should keep in mind that it is not only the North Sea and Skagerak areas that may draw on the Norwegian winter herring and diminish their number on the usual grounds. Extensive spawnings undoubtedly take place, in some years at least, on the Helgeland banks and outside the Lofoten Islands and Vesteraalen (Runnström, 1934; Wiborg, 1950). These grounds are not fished for herring, and the taggings have accordingly given no evidence whether tagged herring may be lost through "dispersal" this way.

To account for the tagged herring disappearing in this manner, we may introduce a dispersal coefficient expressing the quotient between the herring

moving to other grounds and the original number. It is more convenient, however, to use the complement to this quotient, an expression we will term the "gathering coefficient" and denote it by γ. We may assume that the dispersal will be determined from the route the herring takes when leaving the fishing grounds. The natural mortality has by then taken an insignificant toll only and we may regard the gathering coefficient γ and the survival coefficient ϱ as independent of each other. Introducing the parameters γ and ϱ in (4) this expression takes the form:

$$t = T\gamma\varrho \quad \text{where}$$

the product $\gamma\varrho$ denotes the quotient between the returning herring and the original number. As will be seen, within-season recaptures, tagging mortality and shedding effects, are disregarded in accordance with the preceding discussion. The first of these will probably not be quite insignificant except for the spring herring taggings.

Substituting the expressions for (2), (3), and (4) in (1) and re-arranging, we get our stock figure:

$$S = T\gamma\varrho \times \frac{e \times p}{r} \tag{5}$$

If we want the stock expressed in number of individuals, we have to multiply p with the average number of herring per measuring unit:

$$S = T\gamma\varrho \times \frac{e \times p}{r} \times \bar{a}$$

and this expression simply states that the stock is equal to the tagged herring present, multiplied by the ratio of untagged to tagged fish in the catch. This statement is rather self-evident, and if no dispersal existed, the stock calculation would be a rather straightforward task. Let us examine such a case. If we in an experiment tag a number T_1, there will after one year be $T_1\varrho_1$ left when ϱ_1 is the coefficient of survival in the first year. We will assume that one year is amply sufficient for the tagged herring to get thoroughly mixed in the stock. In the second year this tagging yields $r_1^{(2)}$ returns of an amount of e_2p_2 cleared for tags. The stock is then in year 2:

$$S_2 = T_1\varrho_1 \frac{e_2\, p_2}{r_1^{(2)}} \tag{6}$$

For the next year we get with analogous symbols:

$$S_3 = T_1\varrho_1\varrho_2 \frac{e_3p_3}{r_1^{(3)}} \tag{7}$$

If we now in year 2 had tagged an amount of T_2, we could construct another expression for S_3, likewise with analogous symbols:

$$S_3 = T_2\varrho_2 \frac{e_3p_3}{r_2^{(3)}} \tag{8}$$

(7) and (8) yield:

$$\varrho_1 = \frac{T_2 \times r_1^{(3)}}{T_1 \times r_2^{(3)}} \tag{9}$$

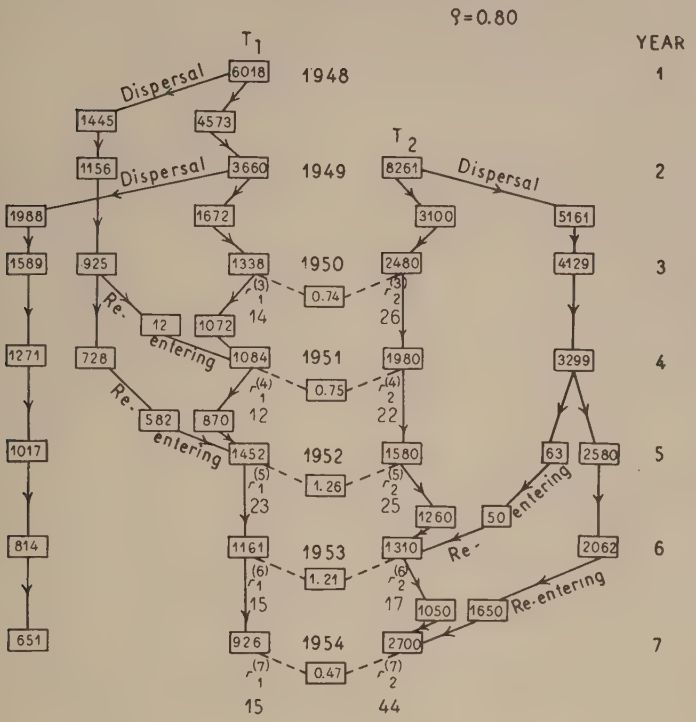

Figure 1.

which together with (6) gives:

$$S_2 = T_2 \times \frac{r_1^{(3)}}{r_2^{(3)}} \times \frac{e_2 p_2}{r_1^{(2)}} \tag{10}$$

This equation (10) is important, because, if we could assume that the herring tagged in a season would disperse in the same manner as the untagged, the same expression (10) would be obtained:

$$S_3 = (T_1 \gamma_1 \varrho_1)\, \gamma_2 \varrho_2 \frac{e_2 p_2}{r_1^{(3)}} \tag{11}$$

$$S_3 = T_2 \gamma_2 \varrho_2 \frac{e_2 p_2}{r_2^{(3)}} \tag{12}$$

From (11) and (12) we derive:

$$\gamma_1 \varrho_1 = \frac{T_2 r_1^{(3)}}{T_1 r_2^{(3)}} \tag{13}$$

which together with (5) yields (10). However, we cannot be sure that the dispersal will be the same since the within-season tags are not evenly distributed in the stock. Instead of (13) we get in this case:

$$\frac{\gamma_2'}{\gamma_2}\gamma_1\varrho_1 = \frac{T_2 r_1^{(3)}}{T_1 r_2^{(3)}} \tag{14}$$

where γ_2 and γ_2' refer to the within-season tags and the stock respectively. The issue is still more complicated because γ_1 may be influenced by re-entering of dispersed herring tagged in the first year. This, however, is a point of minor interest. What is important is that: $\frac{T_2 r_1^{(n)}}{T_1 r_2^{(n)}}$ from year 3 and onwards will be constant if there are no later immigrations of dispersed herring or, in case such immigrations do take place, the herring from the two taggings re-enter in the same proportion. That would be a rather odd coincidence to happen if different proportions of dispersed herring were going into different areas in the two years. By studying a series of $\frac{T_2 r_1^{(n)}}{T_1 r_2^{(n)}}$, we may therefore decide whether dispersals and re-entering have taken place. Figure 1 represents, in diagrammatic form, the idea behind this structure and demonstrates how an irregular series (obtained by the 1948 and 1949 spring herring taggings) may be explained in a rational way. The yearly coefficient of survival is chosen at 0·80 and applies both to dispersed and undispersed herring. Any dispersal after year 3 (1950) is not considered because it would not influence the proportion of the returns in this series and thus unnecessarily complicate the diagram which is shown for the purpose of illustration only.

It is obvious that such dispersal effects, if traced, will seriously affect any calculation of mortality rates and stock. It must be left to a consideration of the results to decide whether such calculations are possible or not.

III. Discussion of Results

Since only the recaptures in Norway are numerous enough to attempt any quantitative treatment, this section will only deal with these data. In the Tables 1 to 5 are shown the distribution in the factories of the recaptures from the different experiments in the years 1950 to 1954. Before 1950 there were too few factories with magnets in Norway and the returns were accordingly too few for statistical treatment. These tables will also serve as an illustration of the development in the building-up of the recovery installations. The first row in the tables gives the year of recapture. In the second row are listed the different experiments. L.H., S.H., and O.H. refer to Large herring, Spring herring, and North coast herring respectively. In this last is also included herring tagged in the Norwegian Sea. The symbols *e* and *p* has the same meaning as explained in the theoretical part. The tables include only tags from factories in which efficiency tests have been made, and will therefore not correspond with the figures given in the text tables in this and the earlier reports (FRIÐRIKSSON and AASEN, 1950, 1952).

Generally speaking we may say that the tags are reasonably well randomly distributed in the catches. In this first treatment, however, we shall not attempt to demonstrate this by any tests.

Table 1

1950

Factory No.	p (hl)	e	$e\,p$ (hl)	1948 S.H.	1948 O.H.	1949 S.H.	1950 L.H.	1950 S.H.	Total
1	147,532	0·97	143,106	4	1	4	0	2	11
2	201,052	0·96	193,010	1	1	2	0	0	4
5	104,929	0·94	98,633	1	1	2	0	0	4
7	123,169	0·87	107,157	1	0	1	0	0	2
12	73,157	1·00	73,157	0	0	2	0	0	2
17	40,349	0·94	37,928	0	0	1	0	0	1
18	230,181	1·00	230,181	0	1	4	0	0	5
23	340,507	0·39	132,798	2	2	4	0	2	10
29	261,024	0·67	174,886	1	0	0	0	0	1
31	415,402	0·89	369,708	1	1	3	0	0	5
42	158,991	0·78	124,013	0	1	1	0	0	2
43	116,040	0·97	112,559	3	1	2	0	0	6
Total	2,212,333	0·81	1,797,136	14	9	26	0	4	53

Table 2

1951

Factory No.	p (hl)	e	$e\,p$ (hl)	1948 S.H.	1948 O.H.	1949 S.H.	1950 L.H.	1950 S.H.	1950 O.H.	1951 L.H.	1951 S.H.	Total
1	160,526	0·97	155,710	1	0	2	0	1	0	3	0	7
2	206,626	0·96	198,361	2	0	3	1	1	1	2	0	10
5	109,226	0·94	102,672	0	0	0	0	0	0	2	0	2
7	125,028	0·87	108,783	0	0	1	2	0	0	1	0	4
11	198,969	0·53	105,454	0	0	0	0	0	1	0	0	1
17	47,465	0·94	44,617	1	0	0	0	0	0	1	0	2
18	249,253	1·00	249,253	2	0	4	0	0	1	6	0	13
23	315,131	0·39	122,901	2	1	4	0	2	0	3	0	12
29	220,189	0·67	147,526	1	0	0	1	0	0	1	0	3
31	418,790	0·89	399,423	1	1	1	5	1	1	7	0	17
35	438,625	0·18	78,953	1	0	1	0	0	0	0	0	2
37	242,557	0·95	230,429	0	1	3	0	0	0	0	0	4
38	258,200	0·59	152,338	0	1	1	1	2	2	2	0	9
40	125,075	0·67	83,800	0	0	0	1	0	0	0	0	1
42	447,319	0·78	348,909	0	3	0	3	2	4	1	0	13
43	181,889	0·97	176,442	1	0	2	0	0	0	1	0	4
Total	3,774,868	0·72	2,705,571	12	7	22	14	9	10	30	0	104

In Table 6a is presented a summary of the total number of recoveries. In the top part of the table are given the year of tagging, the number tagged, and the category of herring. The within-season recoveries are left out. In Table 6b the recaptures are expressed as $^0/_{00}$ returns per million hl. There are two striking features of this table. Firstly, we should normally expect the percentage of recoveries to decrease with time because of the mortality. We notice, however, that most of the experiments do not conform to this rule. In 1953, for instance, we have a general rise in the figures giving the per mille returns per million hl (Table 6b). Secondly, we see that the herrings tagged off the Icelandic north coast and in the open ocean yield relatively more returns than the herrings tagged on the Norwegian coast except for 1948. Generally, the large herring gives the lowest percentage of recoveries. The spring herring tagged in 1950, however, is an exception.

Table 3

1952

Factory No.	p (hl)	e	$e\,p$ (hl)	1948 S.H.	1948 O.H.	1949 S.H.	1950 L.H.	1950 S.H.	1950 O.H.	1951 L.H.	1951 S.H.	1951 O.H.	1952 L.H.	1952 S.H.	Total
1	186,531	0·97	180,935	3	1	1	1	1	2	1	4	1	2	0	17
2	253,455	0·96	243,317	1	1	1	0	1	1	0	4	3	1	0	13
5	125,365	0·94	117,843	0	0	5	0	0	2	0	5	3	0	2	17
7	164,492	0·87	143,108	0	1	0	0	0	1	1	0	5	1	0	9
8	112,826	0·78	88,004	0	0	1	0	1	0	0	1	1	2	0	6
11	153,997	0·78	120,118	1	0	1	0	0	0	0	6	1	0	1	10
15	213,626	0·91	194,400	2	0	3	0	0	2	0	6	2	0	0	15
17	42,226	0·94	39,692	0	0	0	0	0	0	0	0	0	0	0	0
18	243,759	1·00	243,759	3	1	1	1	2	0	4	11	4	1	0	28
20	280,171	0·97	271,766	5	0	2	1	1	2	2	9	5	0	0	27
22	37,244	0·88	32,775	0	0	0	0	0	0	0	1	0	0	0	1
23	456,830	0·87	397,442	1	0	1	1	2	2	2	4	2	0	1	16
29	146,563	0·93	136,304	0	0	1	0	0	0	1	0	1	0	0	3
31	562,801	0·89	500,893	1	1	2	1	1	1	2	1	6	3	9	28
35	472,537	0·35	165,388	1	0	0	0	0	0	1	0	0	0	0	2
37	320,845	0·75	240,634	0	0	0	2	0	1	2	2	4	16	0	27
38	327,947	0·71	232,842	0	0	1	0	0	0	0	2	1	0	0	4
40	121,100	0·74	89,614	0	0	1	0	0	0	0	1	3	2	0	7
42	538,400	0·89	479,176	4	0	1	5	0	1	4	0	9	8	0	32
43	185,133	0·97	179,579	1	2	3	2	0	1	1	6	4	1	0	21
52	328,564	0·88	289,136	0	2	0	0	0	0	2	0	0	11	0	15
Total	5,274,412	0·83	4,386,725	23	9	25	14	9	16	23	63	55	48	13	298

The first of these phenomena may be explained in part by failure of recruitment to the stock in 1953. It is also a fact that the herring in that year were exceptionally large. But that would not account for the rise in the per mille returns per unit of catch. There must also have taken place a re-immigration of dispersed tagged herring which has been on some other grounds in the previous season or seasons. In 1954 the situation seems more normal in corroboration with the fact that the sampling of the herring shows that the recruitment to the stock was good. The returns for the 1949 spring herring, however, shows a marked increase in their relative abundance, showing that a re-immigration must have taken place. It may be of interest to study this in more detail. In Table 7 are presented the expressions equivalent to (14), separately for the spring herring (7a), the large herring (7b), and the north coast herring (7c). Each of the experiments within the different categories is compared with all the others. To the left in this table are given the years of recapture. The top part and the right hand side give the different experiments. The table is then to be read like a co-ordinate system, for instance, the spring herring taggings for 1948 and 1949 give 0·74 in 1950 and 0·47 in 1954. If there were no disturbing effects of dispersal and re-entering, this table should have the following properties: — (1) all the figures should be lower than one; (2) there should be a regular decrease from left to right within each partition; (3) read vertically each column should give the same figure for all years. An inspection of this table reveals such a spreading of the figures, that all the experiments seem to have been effected by dispersal (and re-entering), some very seriously.

If we interpret the evidence furnished by Tables 6 and 7 from the viewpoint of the dispersal hypothesis, the mechanism producing the obtained figures

Table 4

1953

Factory No.	*p* (hl)	*e*	*e p* (hl)	1948 S.H.	1948 O.H.	1949 S.H.	1950 L.H.	1950 S.H.	1950 O.H.	1951 L.H.	1951 S.H.	1951 O.H.	1952 L.H.	1952 S.H.	1952 O.H.	1953 L.H.	1953 S.H.	Total
1	69,351	0·97	67,270	1	0	0	0	0	0	1	0	1	0	0	9	1	0	13
2	112,352	0·96	107,858	0	0	0	0	0	0	1	2	3	0	0	9	0	0	15
5	78,919	0·94	74,184	0	0	0	0	2	1	1	2	1	0	3	5	0	0	15
7	112,380	0·98	110,132	1	1	0	1	0	1	0	0	3	1	1	6	0	0	15
8	94,229	0·78	73,499	0	0	1	0	0	0	0	1	1	0	2	8	0	0	13
11	111,535	0·78	86,997	0	0	3	0	0	0	0	0	3	0	5	14	4	0	29
12	59,332	1·00	59,332	0	1	1	1	0	0	0	2	0	0	2	2	0	0	9
15	146,130	0·91	132,978	2	0	1	0	1	1	1	3	2	0	9	9	0	0	29
16	150,543	0·99	149,038	1	1	0	1	0	1	2	7	1	1	8	9	2	0	34
17	28,318	0·94	26,619	0	0	0	0	0	0	0	0	0	0	1	2	0	0	3
18	171,492	1·00	171,492	2	1	0	0	1	0	0	7	1	0	12	8	0	0	32
20	308,359	0·97	299,108	1	1	3	0	0	1	3	10	0	3	9	7	0	0	38
21	216,065	1·00	216,065	1	1	2	0	0	0	1	7	2	2	8	16	0	0	40
22	39,336	0·88	34,616	0	0	0	0	0	0	1	1	0	0	0	3	0	0	5
23	194,320	0·87	169,058	0	0	0	0	0	1	2	0	2	0	3	14	2	0	24
24	158,064	0·83	131,193	0	1	0	0	0	0	2	1	0	1	0	3	2	0	10
29	163,349	0·93	151,915	0	0	0	0	1	0	0	0	3	0	0	14	0	0	18
31	270,362	0·83	224,400	2	2	0	0	0	2	1	6	6	0	7	27	2	20	75
35	303,340	0·35	106,169	1	0	0	0	1	1	1	1	2	1	0	18	0	0	26
37	222,199	0·75	166,493	0	0	2	3	0	1	1	4	7	1	1	18	0	0	38
38	224,253	0·71	159,220	0	0	1	0	0	0	1	1	0	0	0	4	0	0	7
40	81,903	0·74	60,608	0	0	0	1	0	1	0	0	1	0	0	3	0	0	6
42	312,802	0·89	278,394	2	0	1	2	2	0	1	4	9	5	0	22	0	0	48
43	190,662	0·97	184,942	0	0	0	1	0	2	1	0	6	2	1	11	0	0	24
45	59,066	0·66	38,984	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2
52	88,413	0·88	77,803	1	0	1	0	0	0	0	1	0	1	0	2	0	0	6
55	33,740	0·96	32,390	0	0	0	0	0	0	1	0	0	0	1	2	0	0	4
Total	4,000,814	0·85	3,390,757	15	9	17	10	8	13	22	60	54	18	73	246	13	20	578

Table 5

1954

Factory No.	p (hl)	e	$e\,p$ (hl)	1948 S.H.	1948 O.H.	1949 S.H.	1950 L.H.	1950 S.H.	1950 O.H.	1951 L.H.	1951 S.H.	1951 O.H.	1952 L.H.	1952 S.H.	1952 O.H.	1953 L.H.	1953 S.H.	1953 O.H.	1954 L.H.	1954 S.H.	Total
1	101,349	0·97	98,309	1	1	0	2	0	0	0	0	3	0	0	2	0	0	8	0	0	17
2	177,207	0·96	170,119	0	0	5	0	0	0	0	4	4	1	0	11	0	2	11	1	0	39
5	94,814	0·80	75,851	0	0	0	0	0	0	1	1	0	0	3	4	0	0	7	1	0	17
7	178,288	0·98	174,722	0	1	3	0	0	2	1	1	4	1	2	10	1	0	7	4	0	37
8	121,087	0·78	94,445	2	1	3	0	0	1	0	2	2	0	3	5	0	0	6	7	0	32
9	133,938	0·83	111,169	0	0	0	1	0	0	0	1	0	0	1	3	0	0	5	1	0	12
11	138,650	0·83	115,080	1	0	1	0	1	0	0	1	2	0	2	6	0	1	8	4	0	27
15	193,384	0·91	175,979	0	0	1	0	0	0	0	2	1	1	6	8	1	5	7	5	0	37
16	192,399	0·99	190,475	0	0	4	0	0	1	0	3	2	0	5	16	2	3	10	8	0	54
17	41,546	0·93	38,638	0	0	0	0	0	0	0	2	1	1	0	1	0	0	0	0	0	5
18	243,921	0·95	231,725	1	2	3	3	1	0	0	5	7	0	8	14	2	2	12	5	0	65
20	312,367	0·89	278,007	0	1	1	1	0	0	0	5	3	0	7	16	1	2	11	3	0	51
21	278,424	1·00	278,424	1	0	1	0	0	1	0	3	5	1	4	7	3	1	14	7	0	48
22	53,210	0·94	50,017	0	0	1	0	0	0	0	1	0	0	1	3	0	0	5	4	0	15
23	301,233	0·80	240,986	1	0	1	0	0	1	0	3	3	1	3	16	0	3	9	7	0	48
24	495,000	0·83	410,850	1	1	1	5	1	1	6	4	6	1	2	33	0	1	25	10	2	98
29	270,402	0·80	216,322	1	1	1	2	2	1	1	2	3	0	13	12	2	2	13	2	1	59
31	406,963	0·70	284,874	2	1	7	0	3	1	5	3	4	4	5	28	2	3	22	11	3	104
33	270,789	0·88	238,294	0	1	1	1	1	1	1	1	3	0	7	18	3	0	14	3	0	55
35	417,695	0·68	284,033	0	1	2	1	0	1	1	1	6	2	1	23	0	0	13	0	0	52
37	416,154	0·75	312,116	1	1	4	0	0	0	2	4	4	2	3	13	1	2	11	1	6	55
38	513,120	0·71	364,315	2	0	0	0	0	0	2	2	2	1	6	8	0	4	6	6	8	45
40	177,410	0·82	145,476	0	0	0	0	0	0	1	1	1	2	0	5	0	0	5	0	1	16
42	629,338	0·82	516,057	0	0	1	2	2	2	4	7	13	3	15	36	1	2	24	2	19	133
43	402,404	0·97	390,332	0	0	2	0	0	0	0	8	1	3	4	11	0	3	11	6	10	59
45	171,310	0·66	113,065	0	0	0	0	0	0	0	0	2	1	2	7	0	1	3	0	0	16
52	164,156	0·88	144,457	1	0	1	0	0	0	2	1	2	1	3	10	0	0	5	0	0	26
55	38,071	0·96	36,548	0	0	0	0	1	0	0	0	0	0	1	2	0	0	2	0	0	6
Total	6,934,629	0·83	5,780,685	15	12	44	16	12	13	27	68	84	26	107	328	19	37	274	96	50	1228

Table 6

(a) Number of returns for the different experiments

Year of recapture	1948 6018 S.H.	1948 7475 O.H.	1949 8261 S.H.	1950 9085 L.H.	1950 11,215 S.H.	1950 1827 O.H.	1951 5998 L.H.	1951 9986 S.H.
1950	14	9	26					
1951	12	7	22	14	9	10		
1952	23	9	25	14	9	16	23	63
1953	15	9	17	10	8	13	22	60
1954	15	12	44	16	12	13	27	68

	1951 5076 O.H.	1952 10,295 L.H.	1952 10,763 S.H.	1952 17,308 O.H.	1953 10,080 L.H.	1953 10,046 S.H.	1953 10,181 O.H.
1950							
1951							
1952	55						
1953	54	18	73	246			
1954	84	26	107	328	19	37	274

(b) Per mille returns per million hl

1950	1·30	0·67	1·75					
1951	0·74	0·35	0·98	0·57	0·30	2·03		
1952	0·87	0·28	0·68	0·35	0·18	2·00	0·87	1·41
1953	0·74	0·36	0·61	0·33	0·21	2·10	1·08	1·77
1954	0·43	0·28	0·92	0·31	0·19	1·23	0·78	1·18

1950								
1951								
1952	2·48							
1953	3·14	0·52	2·00	4·19				
1954	2·86	0·44	1·72	3·27	0·33	0·64	4·66	

would be that the mass of herring congregating on the spawning grounds on the Norwegian coast in the winter-time, split up into several bodies which may be separated for many years before rejoining. More likely than not the main part will follow the highway to the feeding grounds stretching from north of the Faroes past the north-eastern Icelandic coast to the Jan Mayen area. Other parts, we know, may enter the North Sea region. Still others may take different courses of which we know nothing. It seems not unreasonable to suppose that when a comparatively small number of tagged herring is injected in the huge stock, these may be carried off in numbers by one of the "stray" bodies before having time to penetrate properly into the main body. This herring may later rejoin as was the case in 1952 with the spring herring tagged in 1948, in 1954 with the spring herring tagged in 1949, and in 1953 with herrings from several of the experiments. Similar examples may also be quoted for the large herring; for instance, the 9th liberation, experiment 8 B at Lotra in 1951 (1010 herrings) gave no returns in 1952, 5 returns in 1953, and 12 in 1954. These examples show clearly that taggings, which perhaps at first seem to be a failure, might well be successful; but it is still an unsolved riddle why the large herring generally should be more susceptible to dispersal than the spring herring. It is more easily conceivable that the tagged north coast herring, being injected more

Table 7

(a) Spring herring

	1949	1950	1951	1952	1953	
1950	0·74					
1951	0·75	2·49				
1952	1·26	4·77	0·61			1948
1953	1·21	3·50	0·41	0·37		
1954	0·47	2·08	0·37	0·25	0·68	
1951		3·32				
1952		3·78	0·48			1949
1953		2·89	0·34	0·30		
1954		3·71	0·68	0·54	1·45	
1952			0·15			
1953			0·15	0·11		1950
1954			0·16	0·11	0·29	
1953				0·89		
1954				0·69	1·85	1951
1954					2·70	1952

(b) Large herring

	1951	1952	1953	
1952	0·40			
1953	0·30	0·63		1950
1954	0·39	0·70	0·93	
1953		2·09		
1954		1·78	2·39	1951
1954			1·34	1952

(c) North coast herring

	1950	1951	1952	1953	
1951	0·17				
1952	0·14	0·11			1948
1953	0·17	0·11	0·08		
1954	0·23	0·10	0·09	0·06	
1952		0·81			
1953		0·67	0·50		1950
1954		0·43	0·38	0·26	
1953			0·75		
1954			0·87	0·62	1951
1954				0·70	1952

directly into the major body on the main highroad, should appear more numerous in the catches. We have, to be sure, similar effects here also, due probably to the fact that the tags have been injected mostly on the very fringes of the distribution. In this connexion it is significant that the taggings in the Norwegian Sea proper in 1951 (the only open ocean tagging comprising a substantial number) gives a higher recapture percentage in the following two years than does the north coast tagging executed in 1951. In 1954 the results are practically the same.

The problems discussed here are very interesting and demonstrate the intricacy of the herring migrations. The explanation offered throws new light on this complex phenomenon, and it also gives a rational explanation to certain irregularities in the age distributions; for instance, that a regularly decreasing year-class may show a sudden rise as we have seen happen time and again in the Norwegian winter herring. But, unfortunately, any exact calculation of the stock strength and the mortality rates is rendered impossible for the present through these complications. The parameters introduced in the theoretical part cannot be eliminated with our present series of observation; but opportunity to do so may well arise by further investigations. At present we have to be content with rough estimates.

For the evaluation of the mortality rate we will disregard the spring herring taggings of 1950 and 1953, all the large herring taggings, and the 1948 north coast taggings since these experiments yield absurdly high or hopelessly low figures when compared with the other experiments (Table 7). We may now obtain an estimate of the yearly survival rate by averaging the remaining figures — assuming that the ups and downs will balance each other in the end.

We get then the following figures: $\varrho = 0{\cdot}79$, $\bar{\varrho}^2 = 0{\cdot}50$, $\bar{\varrho}^3 = 0{\cdot}42$, and $\bar{\varrho}^4 = 0{\cdot}31$. The grand average survival rate will thus be $\bar{\varrho} = 0{\cdot}75$. This figure is not so very far from LEA's average survival rate of $\bar{\varrho} = 0{\cdot}81$, found by analysing a long series of age determinations of the Norwegian winter herring (LEA, 1930). Moreover, the observations do not cover the same period and the greatly expanded fishery in the post-war years may account for some of the discrepancy.

For the stock estimates we may use an indirect approach which will give some information about the stock present on the fishing ground. We know that there is a continuous loss of tags due to mortality and the original tagged amount is the upper limit for the number present on the ground. From this it follows that the experiment giving the highest percentage of returns per unit of catch may be used for establishing an estimate of the lower limit for the fishing mortality. From this may further be calculated the upper limit of the stock level (i.e., stock present on the fishing ground). Using the figures for O.H. in Table 6, we obtain the following values: —

	1951	1952	1953	1954
Fishing mortality %... (lower limit)	1·9	2·2	3·0	5·4
Stock level mill. tons .. (upper limit)	50	40	24	22

Judging from these figures there seems to have been a rapid decline since 1951 of the abundance of herring on the usual winter herring grounds, somewhat checked in 1954. These figures are based on the north coast taggings. We cannot compare these values for every year with the results from the taggings on the Norwegian coast owing to the difficulties mentioned earlier. For 1954, however, the spring herring tagged in 1949 seems to have re-joined in force. Assuming that these have had a yearly reduction of 25% (the survival rate 0·75), we may calculate the probable minimum fishing mortality for these herrings in the same way. We shall then find a value for the fishing mortality of the same order of magnitude as for the taggings on the north Icelandic coast in 1953 (a little lower). The same applies to the 59th liberation (large herring) previously mentioned, the order of magnitude is the same, but this time a little higher. This is corroborating evidence of some importance. These experiments are widely distributed in time and place and are yet linked up fairly well through the estimated mortality rate. Moreover it is in conformity with the dispersal hypothesis which, in fact, explains satisfactorily[1] these rather unexpected results from the taggings and brings some order in an intricate series of numbers otherwise incomprehensible. We must stress that no undue importance should be placed on the stock figures given. They are solely to be interpreted as maxima figures, i.e., that the stock cannot be any larger, provided of course, that our basic assumptions hold good. For that matter the apparent trend might not even be right. It is, however, reasonable to suppose that the estimate for 1954 — with the corroborative evidence — might not be far from the truth, although too high. We might, therefore, conclude that the fishing mortality this year runs about 5–6% and that the stock accordingly lies about 20 million tons.

[1] In broad outlines, the details are not followed up here.

IV. Summary

The irregularities in the series of recapture figures of tagged herring lead to introduction of "a dispersal hypothesis" the principles of which are explained in the theoretical part of the present paper.

According to this hypothesis the total stock of the Atlanto-Scandian herring are split up into several bodies visiting different spawning localities. When leaving the spawning grounds these bodies disperse over the feeding area and may to some extent re-form differently when gathering for the next spawning.

Obviously this circumstance will render stock estimates difficult and uncertain. Long series of observations will be needed to extricate the main features. (It should be borne in mind, however, that the results discussed partly cover a period in which great changes in the spawning influx to the Norwegian coast have taken place.)

The tagging figures show a yearly grand average total mortality rate of 25%. This figure is not very far from LEA's theoretical figure of 19% calculated from age analyses and covering the pre-war years. (In the post-war years the Norwegian winter-herring fishery has expanded considerably.)

With due reservations it is ventured to suggest that a probable estimate of the stock strength of the Atlanto-Scandian herring in 1954 is about 20 million tons and that the fishing mortality accordingly runs to 5–6%.

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On the Causes of the Poor Catches of Baltic Herring on the Finnish Coast in the Summer of 1956

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Introduction

As a rule a good catch is due to one or several age-groups being greater than normal, whereas poor catches result from small age-groups. The incidence and effect of small Baltic herring age-groups have previously been discussed during an investigation of the herring in the farthest corner of the Gulf of Finland (KANERVA, 1930). In his study the shortage of the herring during the summer of 1929 was attributed to the small number of three-year-old herring of the 1926 year-class.

Baltic herring catches during the summer of 1956 were much below the normal level, especially in the Gulf of Bothnia and in the eastern part of the Gulf of Finland. There are no long-term, reliable statistics of catches, and information on the decrease in the catches at the Finnish coast in comparison with preceding years has been obtained from the fishermen orally. Data obtained from Sweden are based on newspaper articles (*Svenska Dagbladet* 1957, OTTERLIND 1957).

Age Composition of Baltic Herring in 1955 and 1956

Material for elucidating the age composition was collected during the voyages made by the research vessel "Aranda" during the summers of 1955 and 1956. Random samples were taken from catches obtained in experimental fishery with a floating trawl. The trawl was a Swedish midwater trawl, the gape from footrope to headrope being 10 m, the mouth 150 sq. m, and the cod-end mesh 10 mm. The experimental fishery was carried out mainly by night when about 1 hour's trawling in the thermocline gave an average catch of 34 kg of herring. The towing speed varied from 2 to 3 knots. Figure 1 shows the stations at which trawl hauls were made.

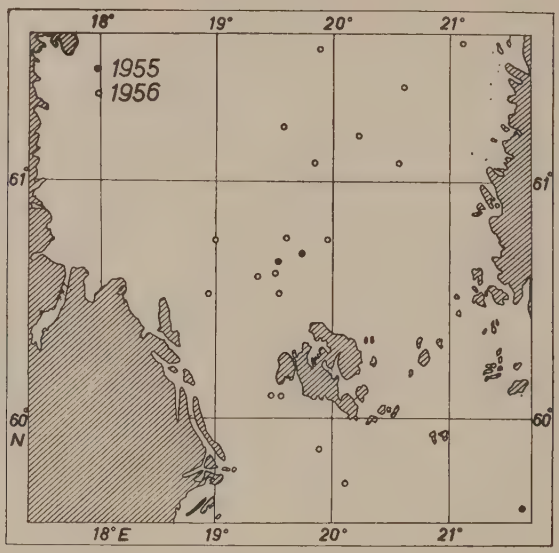

Figure 1. Experimental fishery stations in the southern part of the Bothnian Sea and south of Åland, 1955–56.

Table 1 shows the distribution of the herring in year-classes (%) in three samples obtained in 1955, and 18 samples taken in 1956. The age was determined from the scales and is given in whole years at the beginning of the current growing season, i. e., age = the number of winter-rings. Some young specimens had no scales left, and their age was determined from the otoliths. All the herring classified by the sexual maturity were spring spawners. The following analysis shows the means, calculated from all samples, for the percentage of distribution of the year-classes in these two years.

Age	1	2	3	4	5	6	7	8
1955.....	36·7	17·0	16·3	18·3	8·3	2·7	0·7	0·6
1956.....	13·6	26·1	21·8	19·7	11·6	5·4	1·1	0·4

Figure 2 gives the same distribution. There are two maxima in the 1955 samples the effect of which is also visible in the 1956 samples. The maximum given by the 1-year herring in the former has moved over to the 2-year-class in the 1956 samples. The influence of the minimum for the 2-year-olds in 1955 is seen in the 3-year-olds in the 1956 samples. So the number of Baltic herring born in the summer of 1953 appears to be smaller than the quantity corresponding to the number of individuals of the other age-groups in the samples from both years. The lack of herring in the summer 1956 is thus analogous with the disappearance of the herring in the summer 1929 in the eastern part of the Gulf of Finland (KANERVA, 1930). At that time, too, the decrease of the catches was due to the small number of 3-year-old herring spawning for the first time.

Table 1

Age composition (%) of Baltic herring in three samples taken in 1955 and in 18 samples taken in 1956

Number of rings	Date 1955, July 28.	29.	30.	Date 1956, August 7.	8.	9.	9.	9.	9.	10.	11.	11.	19.	20.	20.	21.	21.	22.	28.	28.	29.
1	81	29	–	–	35	–	1	–	1	9	84	7	20	1	1	4	9	7	42	2	23
2	2	12	37	20	25	19	92	–	15	33	11	27	15	9	15	17	31	31	43	23	44
3	8	21	20	38	11	28	7	8	20	35	5	25	24	22	21	46	23	22	7	35	16
4	7	25	23	28	7	33	–	10	34	22	–	31	19	34	20	15	25	29	5	33	10
5	1	10	14	13	7	12	–	44	13	–	–	9	13	21	31	13	10	8	3	6	6
6	1	3	4	1	7	8	–	36	12	1	–	–	6	9	8	5	1	1	–	1	1
7	–	–	1	–	4	–	–	2	4	–	–	1	2	4	2	–	1	2	–	–	–
8	–	–	1	–	4	–	–	–	1	–	–	–	1	–	2	–	–	–	–	–	–
Total (%)	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Number of fish in sample	198	257	80	71	28	72	70	50	85	100	100	100	100	100	100	100	100	100	100	100	100

Table 2

Temperature (°C) at different depths at stations I–III west of Helsinki in the spring of 1953

Depth in m	Date 24. April	28. April	3. May	10. May	14. May	17. May	22. May	29. May	3. June	5. June	10. June	12. June	15. June	18. June	22. June	29. June
Station I																
0	4·3	4·5	5·8	4·9	5·7	5·6	9·3	5·5	7·2	8·7	13·1	10·5	12·6	13·6	16·8	17·9
2·5	3·7	4·3	5·6	4·9	5·0	5·6	9·2	5·4	7·1	7·9	11·8	10·4	12·5	13·3	15·8	17·1
5	3·4	4·0	4·4	4·9	4·7	5·6	8·8	5·2	7·1	7·7	8·6	10·1	11·2	13·2	13·9	16·9
10	2·3	3·6	4·0	4·9	4·4	5·8	4·6	4·2	6·9	7·5	8·2	9·1	10·0	10·2	8·7	16·6
20	–	2·6	4·4	4·8	3·8	4·2	3·4	2·9	6·5	7·4	7·4	7·5	8·2	7·3	7·1	7·8
25	2·2	2·5	4·0	4·9	3·8	3·2	3·4	3·0	6·5	7·3	6·9	6·2	7·2	5·1	4·7	6·2
Station II																
0	4·2	–	8·2	5·1	6·3	5·9	10·9	5·6	7·1	9·1	13·6	11·7	12·8	14·2	16·4	–
2.5	4·2	–	6·9	5·1	6·2	5·8	10·7	5·5	7·1	8·5	12·9	11·5	12·8	14·1	16·4	–
5	3·6	–	6·2	5·1	5·9	5·1	10·2	5·3	7·1	8·1	8·7	11·4	12·6	13·6	14·7	17·2
10	2·2	–	5·0	5·3	5·8	6·4	4·9	3·8	7·0	7·8	8·6	8·7	9·4	10·6	9·4	15·8
15	2·0	–	4·6	4·4	6·0	6·3	3·8	3·3	4·6	7·3	8·0	7·8	8·5	8·3	8·4	11·3
Station III																
0	5·8	7·7	9·3	5·9	6·8	–	13·4	6·0	8·6	10·5	15·3	12·3	14·3	17·3	18·6	–
2·5	5·3	7·6	6·1	5·8	6·2	–	13·3	4·5	8·3	9·8	14·7	11·9	14·0	16·1	18·5	–
5	4·3	–	6·1	5·8	6·1	–	11·8	4·1	8·2	9·2	9·5	11·8	13·8	15·0	18·5	–
6	3·3	4·8	5·9	5·8	6·0	–	–	–	–	–	–	–	–	–	14·7	–

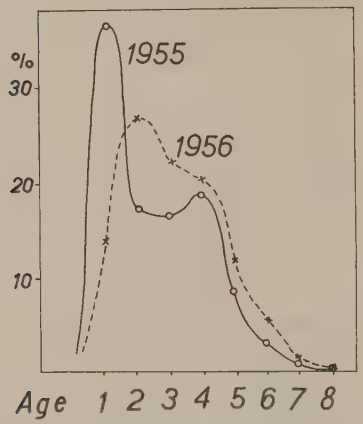

Figure 2. Means of distribution of the year-classes (%) in the samples for 1955–56.

Figure 3. Observation area west of Helsinki. Stations I, II, and III. H = Helsinki, Å = Ådholmen, K = Knapperskär.

On the Spring Spawning of Baltic Herring in 1953

According to KANERVA (1930) the paucity of the 1926 year-class was to be attributed to the storms occurring during the spawning time of the herring during the summer of 1926, their effect on the failure of the spawning being both direct and indirect. MARR (1956), referring to several factors, has shown that in marine fishes the greatest diminution of the year-class occurs at an early stage, either rapidly during a "critical period" or over a longer period. Observations made in the spring and summer of 1953 in the Espoo archipelago west of Helsinki on the temperature of the water and the spawning migrations of the herring offer an explanation for the small numbers of the 1953 year-class and hence for the failure of the herring fishery during the summer 1956.

According to HESSLE (1925, 1937) spring spawners spawn in water of 6° or 7–10°C, while EHNHOLM (1947) says the spawning season of the "herring of the Quark" begins in water of 9°C. EHNHOLM (1951) found that the Baltic herring of the inner archipelago of the Quark spawned in water of 11–13·7°C, those of the outer archipelago in water of 8·2–12·2°C and 13·6–15·2°C and those of the open sea in water of 13·6–16°C. According to RANNAK (1954) developing spawn was found in water of 2·4–17·4°C though in early spring spawning occurred mostly in water of 15–16°C. HESSLE (1937) thought that the variations in temperatures were the reason why the herring did not spawn in a certain area of the inner archipelago.

In 1953 temperature readings were made to the west of Helsinki at three stations (I–III) at different distances from the coast (Figure 3). The results are given in Table 2. The summer-time hydrography of the observation area was characterized by an intensive warming-up in the immediate coastal area, which was retarded as one proceeded outwards from the coast. At the farthest

Table 3

Daily bow-net catches by commercial fishermen near Ådholmen and Knapperskär, west of Helsinki, in the spring of 1953

Ådholmen Date	Catch in kg	Knapperskär Date	Catch in kg
2. May	1890	2. May	1770
4. –	1770	5. –	1020
5. –	1200	9. –	510
6. –	1770	15. –	5920
9. –	360	16. –	2220
12. –	630	17. –	3750
13. –	30	18. –	2185
16. –	300	19. –	1195
20. –	60	20. –	1015
21. –	630	21. –	740
23. –	90	22. –	690
28. –	75	27. –	690
29. –	240	28. –	270
1. June	1410	30. –	670
2. –	660	1. June	1330
8. –	150	4. –	420
11. –	840	5. –	270
13. –	600	8. –	440
17. –	1350	10. –	1500
18. –	1230	13. –	930
		18. –	2130
Total	17,135	20. –	105
		23. –	1460
		26. –	775
		30. –	780
		Total	32,785

station (I) it was possible to observe a distinct difference between the bottom water, which remained cold, and the warm water of the surface. At the middle station (II) this difference was also noted. On the other hand, temperature fluctuations were very sudden at the station (III) nearest the coast. Temperature changed from cold to warm and back again three times during May and June, the cold periods being shorter than the warm periods.

According to commercial fishermens' bow-net catch statistics, no fish had been caught by 28. April near station (III) by the coast. A total of 445 kg of herring was caught there from 1. to 22. May, after which the bow-net was moved further on, the area being considered unprofitable. According to the catch statistics given in Table 3 the bow-net near Ådholmen (level with station II) caught 17,135 kg of herring between 2. May and 18. June. At Knapperskär, which lies level with station I, one bow-net gave a total of 32,785 kg of herring during the period 2. May to 30. June.

Similar differences were found during a fishing experiment carried out in these areas. The nets used were 6 m deep and 30 m long and were put out in the usual way, anchored at both ends, on the bottom of the shallows where the herring spawn. The nets reached from the surface to the bottom. The results are given in Table 4. The smallest amount of fish was caught at the station (III) nearest the coast, where the first net-catches were obtained on 25. April. From the data given in Table 4 the following analysis can be made to compare the catches at the three stations.

Table 4

Results of the fishing experiment west of Helsinki in the spring of 1953

Station I Level of fish in the net	May 17.	June 8.	June 10.	June 12.
1–2	7	–	–	189
2–3	21	1	20	336
3–4	21	1	59	381
4–5	22	4	140	360
5–6	4	8	203	456
6–7	–	7	286	651
Total No. of fish	75	21	708	2373

Station II	May 14.	May 17.	May 22.	June 3.	June 5.	June. 10.
1–2	48	14	15	1	–	–
2–3	176	185	69	2	1	–
3–4	90	208	66	79	13	1
4–5	40	161	67	26	1	6
5–6	12	123	51	1	2	15
6–7	6	38	18	2	–	22
Total No. of fish	372	729	286	111	17	44

Station III	April 25.	April 28.	April 29.	May 3.	May 10.	May 12.	May 14.	June 10.
0–1	5	2	2	–	–	–	–	–
1–2	10	5	27	–	10	4	3	–
2–3	4	2	9	6	10	3	7	–
3–4	2	–	4	–	10	–	4	–
4–5	–	–	–	–	3	–	–	–
5–6	–	–	–	–	–	1	–	–
Total No. of fish	21	9	42	6	33	8	14	–

Table 5

Sexual maturity of the Baltic herring in samples taken west of Helsinki at various stations in the spring of 1953 (%)

Station	III	III	II	III	II	III	II	II	II	II	II
Date / Maturity stage	April 27.	May 2.	May 4.	May 9.	May 12.	May 16.	May 26.	May 30.	June 6.	June 8.	June 17.
I	–	–	–	2	–	6	22	3	1	–	–
II	5	11	4	13	6	15	10	4	6	5	1
III	6	10	6	15	9	22	16	6	16	4	1
IV	22	14	28	51	51	42	33	41	50	13	7
V	67	65	62	19	33	15	14	43	27	13	20
VI	–	–	–	–	1	–	5	3	–	60	51
VII	–	–	–	–	–	–	–	–	–	5	20
VIII	–	–	–	–	–	–	–	–	–	–	–
Total %	100	100	100	100	100	100	100	100	100	100	100
Number of fish in sample	187	224	188	246	212	233	112	151	215	108	141

Date	Station	Catch
14. May	III	14 fish/2 days
14. May	II	372 fish/2 days
17. May	I	75 fish/2 days
17. May	II	729 fish/3 days
10. June	III	0 fish/2 days
10. June	II	44 fish/2 days
10. June	I	708 fish/2 days
12. June	I	2373 fish/2 days

The herring was thus moving very close to the coast at the end of April. New shoals continued to arrive until the end of June. A great number of them remained at the edges of the farthest reefs and the farthest shallows, only a few reaching the nearest reefs and the immediate vicinity of the coast. This innermost area constitutes, as it has done from ancient times, a well known spawning area for the Baltic herring (HALME, 1948).

The fishing experiment also gave some data on the vertical distribution of the herring, as the catch was counted at metre intervals along the depth of the net. The results are given in Table 4. According to Table 4 the herring appeared on the surface (from 0 to 4 m) at the end of April at the station nearest the coast. A movement to the deeper layers of water occurred at the beginning of May, but did not continue right down to the bottom. At station II, about 4 km further out, the movement to deeper water layers had already started when the fishing experiment was begun there in the middle of May. At the end of May and the beginning of June herring were caught in the entire depth of the net. The shoals descended to the bottom in the first half of June. At station I the movement to the deeper water layers was found to have taken place already in the middle of May when fishing was started here. The movement to the bottom took also place at the beginning of June.

In the random samples taken at the same time from bow-nets, spawning fish were found for the first time in the sample of 9. May, which had been taken from the bow-net close to the innermost station. The actual spawning cannot, however, be considered as having commenced until 8. June, to judge from the sample taken on that date from a bow-net level at station II (Table 5).

The temperature of the water, when shoals of herring migrated to the coast, was 6°C at the surface and below 4°C at the bottom at a depth of 6 m at station III near the coast. The conditions remained practically unchanged until the middle of May. Although the temperature had risen higher in between, it was only a little higher than 6°C on 14. May, from the surface to the bottom.

On 10. June at station II it was noted that the herring had descended to the bottom into water of some 9°C, the temperature of the surface water having risen to 13°C. At the same time the shoals descended to the bottom of the shallows near station I into water of 8–9°C. Hence, the Baltic herring, entering the inner archipelago in the spring of 1953, looked for water of a suitable temperature for spawning farther away than the shoals close to the coast. The temperature near the coast was, because of sudden changes, only a little higher than 4°C even as late as the end of May. On the other hand, the herring which had descended to the bottom to spawn near stations I and II were caught, according to the data in the literature, in water suitable for the spawning of

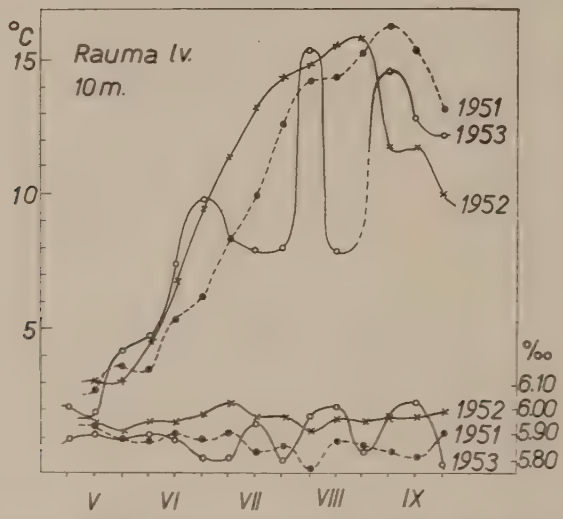

Figure 4. Temperature (°C) and salinity (‰) at a depth of 10 m at the lightvessel "Rauma" in the summer months of May–September for 1951–53.

spring herring. Thus unsuitable temperature or the sudden temperature changes were probably the reasons preventing early spawning close to the coast.

Figure 4 gives temperature and salinity observations taken in May-September in 1951–1953 at a depth of 10 m at lightvessel "Rauma" seaward of the spawning shoals of the Bothnian Sea (GRANQVIST, 1954, 1955). The depth was chosen in accordance with the average spawning depth of the Baltic herring (HESSLE, 1925; KANERVA, 1930; EHNHOLM, 1951). Compared with the years 1951–1952 the temperature and salinity were practically normal in the spring of 1953 until the end of June. Marked fluctuations in the thermocline occurred, on the other hand, from the beginning of June to the end of August. Similar changes were observed in the summer of 1926 in the farthest corner of the Gulf of Finland at lightvessel "Werkkomatala" (GRANQVIST, 1926). According to HJORT (1926) the prerequisite of a good age-group is that development of the spawn, the young fish, and the animals they use for food are suitably interconnected. Disruption of this relationship is probable in areas where the changes in hydrographic conditions are sudden and pronounced.

Summary

Catches of Baltic herring were especially small on both the Finnish and the Swedish coasts in the summer of 1956. Fishing experiments carried out principally in the Gulf of Bothnia indicated that this is attributable to the poor 1953 year-class. Observations west of Helsinki show that the spawning of the herring in the area of the inner archipelago was hampered either by unfavourable water temperature during the spawning period or by the sudden temperature changes occurring at that time. This is assumed to be the basic reason for the poor 1953 year-class.

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On the Appearance of Rings on Herring Scales

By

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Introduction

One of the problems confronting workers on the herring in the North Sea is to evolve a method of separating the various stocks of fish in the area. With this problem in view, a study of the types of annual ring appearing on the herring scale was begun, based on the idea that the rings may be capable of division into various categories and these categories would be representative of the stocks. The material used in this work was drawn mainly, but not entirely, from the East Anglian herring fishery.

Lea (1929) was the first to show that differences existed in the appearance of the annual ring on scales taken from different herring. In Norwegian herring Lea separated the narrow and sharp rings of "Northern Type" and the wide and diffuse rings of "Southern Type". Later investigations (Runnström, 1936) confirmed Lea's hypothesis.

In attempting to define the type or types of annual rings in the East Anglian herring considerable difficulties were encountered. The following account of some of the results is given with the full realisation that considerably more work is needed before all the features can be fully explained.

The scales described in this work were taken from the routine sampling work on the East Anglian herring fishery carried out at the Fisheries Laboratory, Lowestoft and only herring of maturity stage V and VI were used. In the routine sampling the scales were taken from an area above the pectoral fin. Only when there were no scales in this area were scales taken from another area on the body. In addition to this material, scales from eleven positions as shown in Figure 1, were taken from fifteen individual fish. These scales were primarily taken to show the differences in the appearance of the annual rings between the scales when comparing the eleven scales taken from one fish.

It is difficult to describe the appearance of the ring, especially as there can be no precise division between the various types. Therefore the very loose division into "wide" rings and "narrow" rings has been used in this paper. By narrow rings it is meant that the ring is often fine, clear cut, and may even show signs

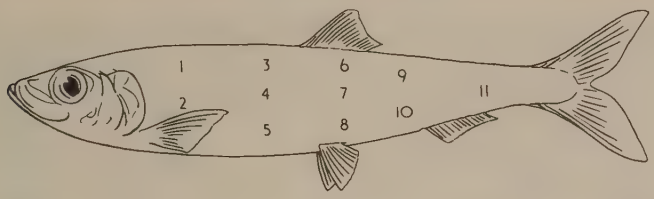

Figure 1. The eleven positions on the herring from which scales were taken.

of breaks in the striae. On the other hand, a wide ring is more diffuse in its appearance and the striae often appear to bend and not break and the ring has no clearly defined edge to it. In Figures 2 and 3, the two types are shown as photographed under a phase contrast microscope. Here the difference in the bending and joining of the striae in the hard or narrow and the soft or wide rings can be seen.

Before discussing the true annual rings, it is necessary to discuss in some detail the accessory rings found on the herring scales, as it was discovered that they play an important part in the final appearance of the annual ring.

Accessory Rings

Accessory rings have been observed in different fishes by many workers. They have been called "false", "secondary", "subsidiary", and "adventitious" rings. It has been assumed that they represent accidental, non-periodic checks in growth. SAVAGE (1919) and others, using polarized light, observed that such rings break the gradual change in width of alternate light and dark concentric bands. It is generally admitted that they are less distinct than the annual rings, although very similar to them and some authors found difficulties in distinguishing the accessory rings from the annual ones. MURAT (1935) however, observed in the Algerian pilchard that they can be more distinct than the true ones, and in our work it was noticed that the accessory rings can be at least as distinct as the annual rings or even more so. (When comparing the two types of ring, polarized light was used for the identification of the annual ring.)

As well as the true annual ring and the accessory ring, other structures which appear as irregularities on individual scales and are often incomplete rings, are found. These were grouped under the heading of "faults" and were neglected.

It was noticed that the accessory rings were present on nearly all the scales from each of the eleven positions on the fish, and SAVAGE (1919) noted that these rings were common to all the scales of an individual. In Figure 4 (a–k), a set of scales from one fish is shown to illustrate the consistency in the presence of accessory rings (Figure 4 d). In this set it is possible to follow the occurrence of a pair of accessory rings inside the first growth zone of all scales although their character varies. The variation in appearance of the annual rings between scales can also be seen in this series.

MURAT (1935) considered that faults represented lesions produced on the scale as a result of some physical damage to the fish and were usually localized.

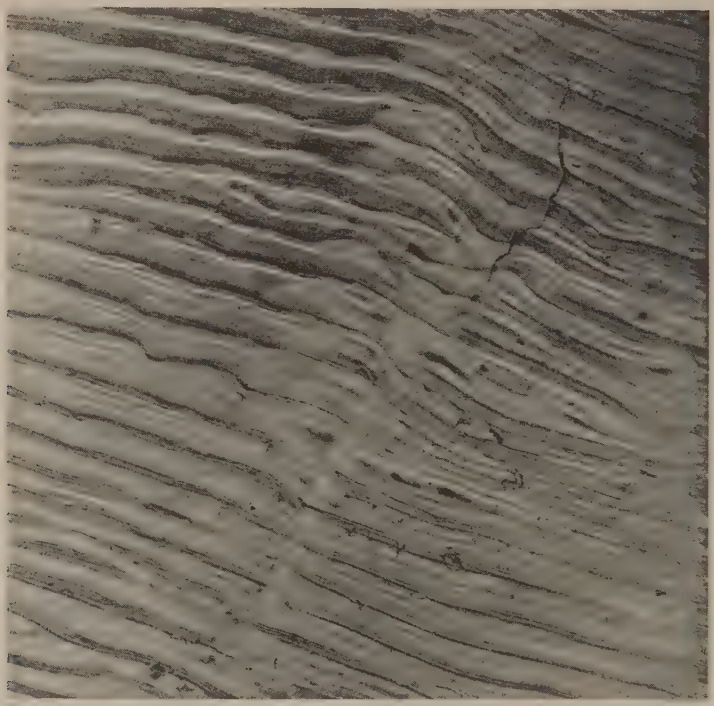

Figure 2. Photograph of a wide annual ring taken under a phase contrast microscope.

This explanation is accepted for the faults, but we cannot agree that the accessory rings result from the same cause, although they may be superficially like faults. Some of the accessory rings which are very clearly defined and which will be called sharp structures have undoubtedly been classified as faults by many workers. The criteria used in this work for distinguishing true faults from the so-called sharp structured accessory rings were as follows.

1. A fault is rarely a complete ring but a sharp accessory is complete from the base of the scale on one side to the base on the other. The striae are broken or at least sharply bent and change direction, both in the sharp structured accessories and the faults.
2. Whereas a fault appears on scales from a relatively small area of the fish, the sharp structures appear in the same position on the scales taken from any part of the fish. The sharp appearance may, however, be softer on some scales from the same fish. For instance there is a clearly defined sharp accessory in the second growth zone in Figure 4h. On other scales from the same fish (Figure 4a) an accessory which is softer in appearance is found in the same position.
3. Finally the sharp structured accessories produce a break in the gradual change in width of light and dark bands when viewed under polarized light,

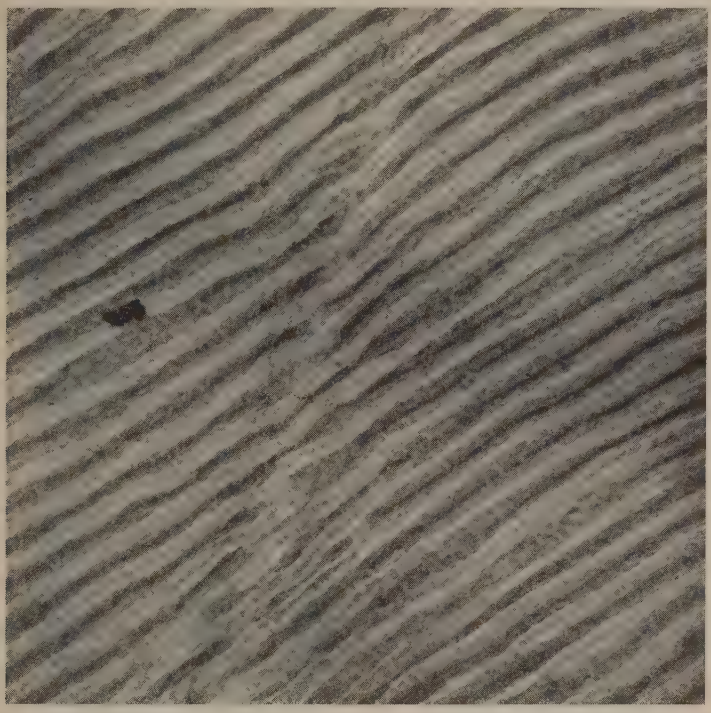

Figure 3. Photograph of a narrow annual ring taken under a phase contrast microscope.

and on the exposed external part of the scale a ring is always found in the same position as the sharp accessory on the striated part of the scale. This can be seen in Figure 5a where there is a sharp accessory in the second growth zone of the striated part (posterior field) of the scale.

Apart from the obvious faults, the appearance of the accessory rings found on herring scales varies from the soft, ill-defined accessory mentioned earlier to the clearly defined sharp accessory which may be confused with the true fault as has been described.

Accessory rings occur very frequently in herring from the Southern Bight and often appear paired with the annual rings. As the accessory rings show a tendency to repetition on consecutive growth zones (in Figure 5b this tendency is shown), the total number found in a sample of North Sea herring scales is very great. In all, nearly 400 scales were examined for the presence of accessory rings. These scales gave a total of 1822 annual rings and 950 accessory rings. In some of the scales accessory rings were not obvious, so the actual estimate should probably be higher than the above figures. One sample of East Anglian herring analysed separately by each of the authors is shown in Tables 1 and 2. The number of accessories given by RICHARDSON tend to be higher than those given by MUZINIC because the former observer counted accessories which were

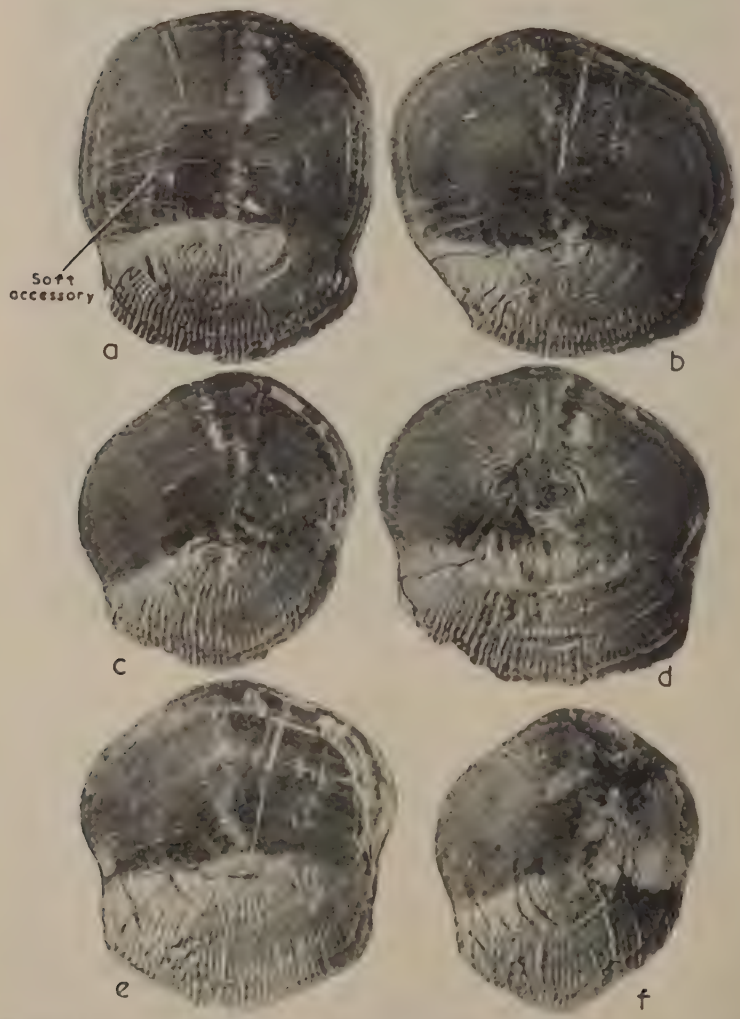

Figure 4 (a - f). A set of eleven scales taken from the same fish from the positions indicated in Figure 1.

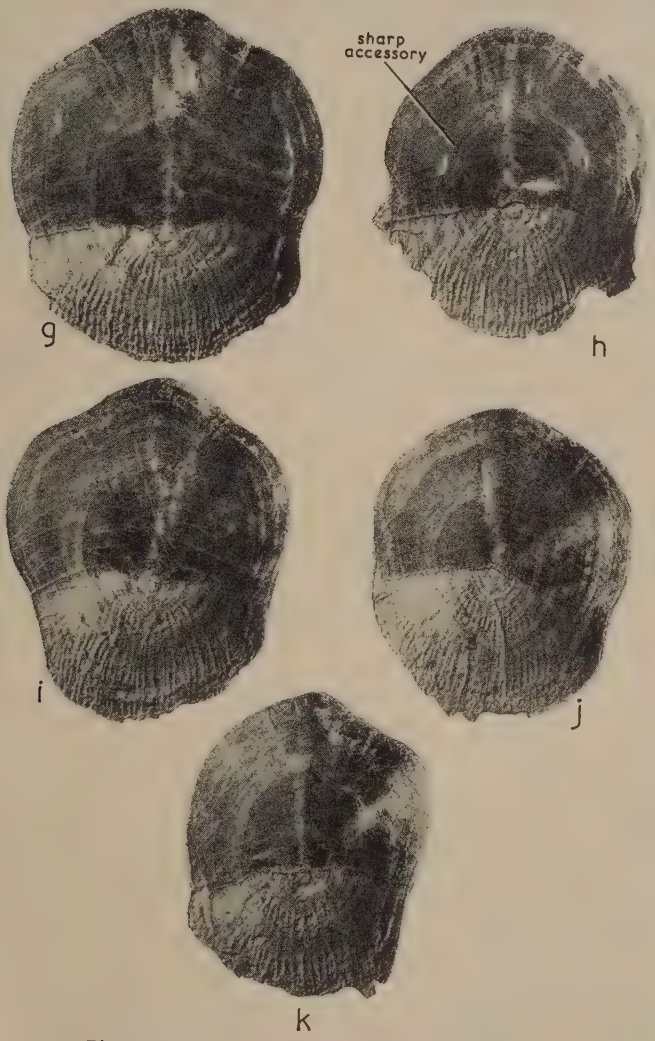

Figure 4 (g – k). See explanation on opposite page.

Table 1

Sample XLT1, read by R. Muzinic

Certain scales are not included due to difficulty of interpretation

No. of fish	Number of accessories	Growth zones in which rings occur
2	2	1, 2
3	3	1, 2, 3
4	3	1, 2, 3[1]
5	3	1, 2, 3
7	3	1, 2, 3
8	3	1, 2, 3
9	3	1, 2, 3
10	3	1, 2, 3
	3?	?
11	2	1, 2, 3
12	3	1, 2, 3
14	4	1, 2, 3, 4
16	2	1, 2
17	3	1, 2, 3
18	3	1, 2, 3
19	4	1, 2, 3, 4
20	3	1, 2, 3
21	3	1, 2, 3
	3?	?
22	2	1, 2, 3
23	3	1, 2, 3
24	3	1, 2, 3
25	3	1, 2, 3
26	2	1, 2
27	2	1, 2
28	2	1, 2
	3?	?
29	2	1, 2, 3
30	2	1, 2
31	2	1, 2
32	2	1, 2
	?	?
33	2	1, 2
34	2	1, 2
35	3	1, 2, 3
38	3	1, 2, 3
40	2	1, 2
41	4	1, 2, 3, 4
42	4	1, 2, 3, 4
43	2	1, 2
44	2	1, 2
45	2	1, 2
46	3	1, 2, 3
47	2	1, 2
49	2	1, 2
50	3	1, 2, 3
51	2	1, 2
52	2	1, 2
	4?	?
53	3	1, 2, 3, 4
55	2	1, 2
56	2	1, 2
	3?	?
57	2	1, 2, 3
58	3	1, 2, 3
59	2	1, 2
60	3	1, 2, 3
62	2	1, 2
63	2	1, 2
65	3	1, 2, 3[2]
66	2	1, 2
67	2	1, 2
68	2	1, 2
70	2	1, 2
71	2	1, 2
	4?	?
73	3	1, 2, 3, 4
76	2	1, 2
77	3	1, 2, 3[2]
79	3	1, 2, 3[1]
80	3	1, 2, 3[3]
81	2	1, 2
82	2	1, 2
83	4	1, 2, 3, 4[1]
84	3	1, 2, 3
85	3	1, 2, 3
86	2	1, 2
88	3	1, 2, 3[2]
89	3	1, 2, 3
90	3	1, 2, 3[2]
91	2	1, 2
92	3	1, 2, 3
93	2	1, 2
94	4	1, 2, 3, 4[2]
95	4	1, 2, 3, 4[2]
96	2	1, 2
97	3	1, 2, 3[2]
98	2	1, 2
99	2	1, 2

[1] Two accessories involved.
[2] Probably more than one accessory involved.
[3] More than one acessory may be involved.

Table 2

Sample XLT1, read by I. D. Richardson

(In this analysis the number of accessories is larger than in Table 1 because those rings which appeared compound for at least part of their length were included as an annual ring with an accessory).

No. of fish	Annual rings excluding outer edge	Number of accessories	Growth zones in which accessories occur	No. of fish	Annual rings excluding outer edge	Number of accessories	Growth zones in which accessories occur
1.....	–	–	–	51.....	3	3	1, 2, 3
2.....	6	3	1, 2, 3	52.....	2	2	1, 2
3.....	6	5	1, 2, 3, 4, 5	53.....	6	3	1, 2, 3
4.....	7	5	1, 2, 3, 4, 5	54.....	5	2	1, 2
5.....	4	3	1, 2, 3	55.....	5	3	1, 2, 4
6.....	–	–		56.....	8?	3	1, 2, 3
7.....	6	3	1, 2, 3	57.....	7?	3	1, 2, 3
8.....	6	3	1, 2, 3	58.....	3	3	1, 2, 3
9.....	3	3	1, 2, 3	59.....	4	2	1, 2
10.....	2	–	–	60.....	4	3	1, 2, 3
11.....	7	5	1, 2, 3, 4, 5	61.....	6	2	2, 3
12.....	3	3	1, 2, 3	62.....	2	2	1, 2
13.....	3	3	1, 2, 3	63.....	3	–	–
14.....	7	5	1, 2, 3, 4, 5	64.....	9	3	1, 2, 3
15.....	6	4	1, 2, 3, 4	65.....	3	3	1, 2, 3
16.....	7	2	1, 2	66.....	10?	2	2, 3
17.....	8?	4	1, 2, 3, 4	67.....	3	1	1
18.....	4	4	1, 2, 3, 4	68.....	3	1	1
19.....	8	4	1, 2, 3, 4	69.....	3	0	0
20.....	4	4	1, 2, 3, 4	70.....	8	2	1, 2
21.....	3	3	1, 2, 3	71.....	5	4	1, 2, 3, 4
22.....	3	3	1, 2, 3	72.....	6	2	1, 2
23.....	6	4	1, 3, 4, 5	73.....	4	4	1, 2, 3, 4
24.....	6	3	2, 3, 4	74.....	5	3	1, 2, 3
25.....	3	3	1, 2, 3	75.....	5	2	1, 2
26.....	2	3	1, 2, 3	76.....	4	2	1, 2
27.....	8?	3	1, 2, 3	77.....	–	–	–
28.....	8?	2	1, 2	78.....	8?	3	1, 2, 3
29.....	9?	5?	1, 2, 3, 4, 5	79.....	5	3	1, 2, 3
30.....	3	3	1, 2, 3	80.....	3	2	1, 2
31.....	3	2	1, 2	81.....	3	2	1, 2
32.....	8	2	1, 2	82.....	3	1	1
33.....	3	2	1, 2	83.....	4	3	1, 2, 3
34.....	3	3	1, 2, 3	84.....	6	3	1, 2, 3
35.....	4	3	1, 2, 3	85.....	3	3	1, 2, 3
36.....	3	3	1, 2, 3	86.....	3	3	1, 2, 3
37.....	3	3	2, 3, 4	87.....	3	2	1, 2
38.....	4	4	1, 2, 3, 4	88.....	4	3	1, 2, 3
39.....	2	3	1, 2, 3	89.....	4	3	1, 2, 3
40.....	3	1	1	90.....	8?	3	1, 2, 3
41.....	5	5	1, 2, 3, 4, 5	91.....	3	2	1, 2
42.....	9?	3	1, 2, 3	92.....	4	3	1, 2, 3
43.....	3	3	1, 2, 3	93.....	3	2	1, 2
44.....	3	3	1, 2, 3	94.....	4	4	1, 2, 3, 4
45.....	6	1	2	95.....	4	3	1, 2, 3
46.....	5	5	1, 2, 3, 4, 5	96.....	2	2	1, 2
47.....	3	3	1, 2, 3	97.....	3	3	1, 2 3
48.....	2	2	1, 2	98.....	4	2	1, 2
49.....	8?	2	1, 2	99.....	2	2	1, 2
50.....	8	3	1, 2, 3	100.....	3	2	1, 2

partially compounded with the annual ring. MUZINIC did not count these rings. Accessory rings were not found in the first growth zones on all scales which possessed one or more paired rings but where they were found in the first zone they usually appeared at some distance inside the annual rings. In the fourth and later zones the accessory rings were infrequently found.

As a decrease in growth coincides with sexual maturity, it may be said that the disappearance of the paired rings coincides mainly with the onset of first sexual maturity. The majority of herring in the region mature in their 3rd or 4th year (HODGSON, 1929) but a proportion of the fish, particularly immigrants, undoubtedly mature at a greater age. The presence of accessory rings before sexual maturity suggests that the accessory ring cannot be a consequence of spawning. In a small percentage of the herring examined accessory rings were found in a large number of growth zones. It is interesting that these fish showed a more uniform growth-rate and are probably immigrants. It is suggested that the time of sexual maturity and consequent growth reduction (where this occurs) is related to the number of zones on which accessory rings occur. There also appears to be a relationship between the position of the accessory within the first growth zone and the total number of accessories on the scale. If the accessory ring or rings are located early in the first period of growth, accessories are usually found in more growth zones than if the accessory is close to the first annual ring. As the accessory is usually at a greater distance within the first annual ring in those fish which have a large first year's growth, the number of zones with accessory rings is probably a function of the fish's growth in the same way as the time of onset of sexual maturity.

Paired rings were also observed in other clupeoids. Some authors assumed that one of these rings could be connected with the spawning. Here the difficulty arose, how to explain the pairs of rings appearing before the first sexual maturity. ZAMAKHAEV (1940) and TCHOUGOUNOVA (1940) called the rings appearing close to the annual ones "rings of displacement". In their opinion, such rings are caused by a slight displacement of the scale in its skin pocket. TCHOUGOUNOVA found in the shad *Caspialosa saposhnikovi* that the distinctive character of the rings of displacement is their more or less turning of the whole zone of the scale in the region of such a ring in relation to the base line, while the further parts of the scale have again a regular disposition. In her opinion, displacement rings do not always coincide with the annual ones and in such cases one isolated ring appears. Up to three rings may appear inside the first zone, according to TCHOUGOUNOVA and were called "juvenile" rings. They were not constant in position. They sometimes appeared not far from the centre, and sometimes close to the annual ring. From this TCHOUGOUNOVA concluded that irregular biological phenomena caused their appearance. The juvenile rings were not always present.

Such an explanation of the origin of the paired rings does not seem to be acceptable as, in our material, one accessory ring forming a pair with one annual ring appears in the majority of the scales from the same fish, and also on the same scale, more than one paired ring may be present. It is therefore difficult to accept that a general and repeated shifting of the scales can take place or if it does why such shifting should occur less in the older fish. In *Caspialosa saposhnikovi* TCHOUGOUNOVA (1940) found that from 272 specimens 45% had an accessory in the second growth zone, 22% in the third, and 2–3% in the fourth and fifth zone. The accessory rings appearing in the first growth zone were not taken into account. It is interesting to note here that TCHOUGOU-

NOVA, judging from the spawning marks on the scales, concluded that these fish attain sexual maturity at two (especially in the males) and three years old. Thus in this species the paired rings disappear roughly on the onset of sexual maturity.

Although the hypothesis that the accessory rings are due to the shifting of the scales is very attractive when explaining the paired nature of certain rings towards their apex, ("casquette"), it appears to need confirmation. A full understanding of the formation of accessory rings is highly desirable but at present it is assumed that they are caused by periodic checks in growth resulting from environmental or metabolic changes. If this explanation is true, and at the moment there is certainly no proof of it, the timing and appearance of the accessory rings may reveal something of the part played by the external environment in the early life of the fish.

Variation in the Appearance of a Ring on Scales taken from the same Fish

The annual rings on scales taken from the same fish rarely have the same general appearance. LEA (1929) noticed a difference in the appearance of annual rings on different scales taken from the same fish. When comparing the same ring on all the scales taken from one fish, it was noticed that some of the rings were wider than others and some showed extensive breaks of the striae which gave the ring a very sharp appearance. In Figures 5c and 5d, two scales from areas 1 and 6 of one fish are shown as an example of how great the difference in the appearance of the ring on two scales from the same fish can be. In area 1, all the rings are wide and more diffuse while in area 6 they are narrower and less distinct. Other examples are seen in Figure 4a–k.

It has already been mentioned that many of the annual rings were accompanied by accessory rings and these accessory rings also differ in appearance on different scales taken from one fish.

In Figures 5e and 5f, two scales from the same fish are shown. On the big scale shown in Figure 5e the second ring and its accessory can be followed along their whole length from one side of the scale to the other. On the smaller scale in Figure 5f it is difficult to distinguish the accessory ring. After the second annual ring, accessories can be seen in Figure 5e but it is not possible to see them in the later growth zones in Figure 5f. The position and occurrence of the accessory ring in relation to the annual ring appears to alter the appearance of the annual ring. This is discussed later.

These differences which have been found between scales on the same fish make it difficult to use the ring type or appearance as diagnostic of the different conditions under which the individual has lived. The use of the ring type as a method of assigning an individual fish to a group or race in the southern North Sea, is therefore considered of little value.

Differences in Appearance within one Ring on the same Scale

It was also found that an individual ring can be wider in one place than in another. In Figure 5c, it can be seen that all the rings in the region of the first annual ring are wider on one side of the scale than on the other. In Figure

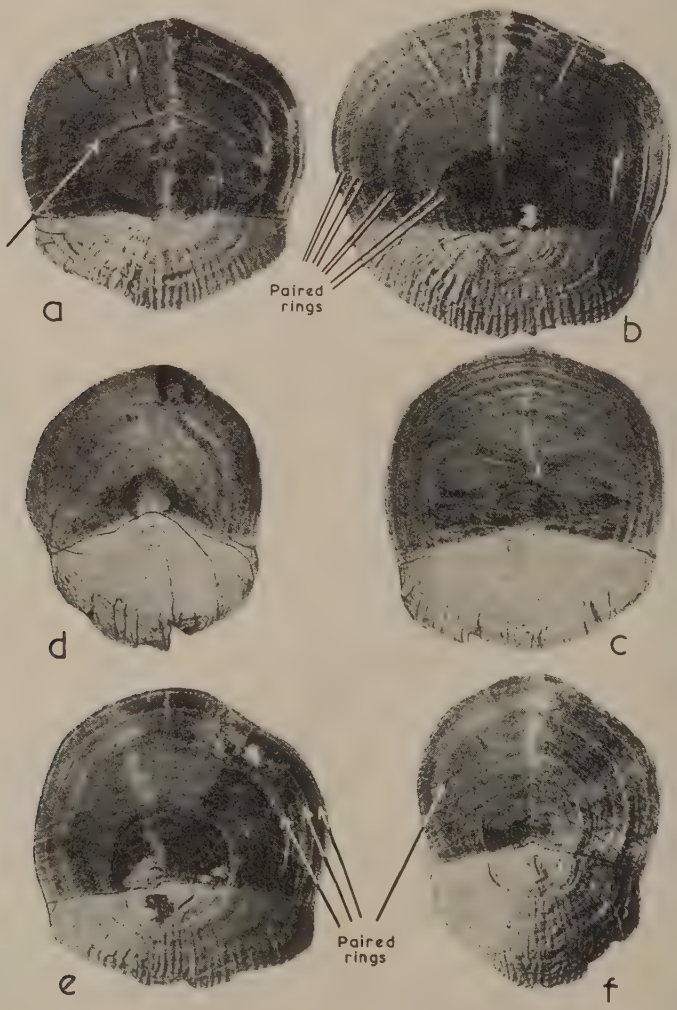

Figure 5. (a) Herring scale showing a sharp accessory in the second growth zone. (b) An illustration of the manner in which accessory rings are often found in many of the growth zones of a scale. (c) A scale taken from area 1. (d) A scale taken from area 6 of the fish from which the scale in (c) was taken. (e) Large scale taken for comparison with the small scale in f. (f) Small scale taken from the same fish as that shown in (e).

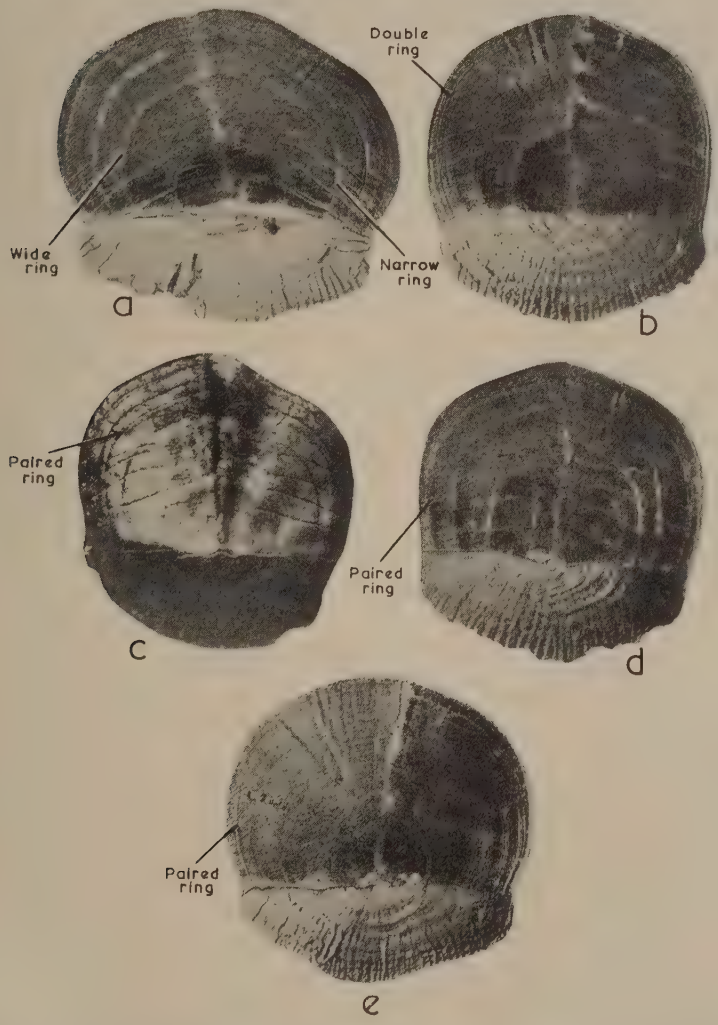

Figure 6. (a) A scale showing the difference in appearance of the rings on different sides of an asymmetric scale. (b) The fourth ring is double on the left side but on the right side it appears as a single ring. (c) A scale on which the third annual ring appears to be compound on one side. (d) and (e). Examples of scales in which a single ring without accessory is followed by a wide growth zone and a compound or even paired ring.

6a, it is possible to see that on the left-hand side the first and second rings, as well as the accessory ring inside the first annual ring, are wide whereas on the right-hand side of the photograph they are narrow.

It was noticed that some of the rings in the material examined were double for a part of their way round the scale but other portions of the same ring did not show this double nature. For instance, in Figure 6b the fourth annual ring is double on the left side and in its apical part but on its right side it is hardly possible to discover any trace of this double nature.

In these instances where there were differences in the structure between different places on the same ring, the scale had an asymmetric appearance, or if the whole scale was not asymmetric, at least some of the growth zones were.

The concept of asymmetry affecting the form and spacing of the annual rings on the scale is not new and anyone who has worked on herring scales will have noticed the crowding of rings on the smaller part of the scale.

Effect of Scale Dimensions on the Appearance of Rings and the Fusion of Rings

The differences in the appearance of rings on the scales taken from one fish and the differences occurring within the same ring lead us to suppose that the appearance of the ring is modified by, and therefore partly due to the shape of the scale and the relative size of the growth zones. Taking this argument to its conclusion it would be expected that wide and diffuse rings observed on one scale could appear as narrow and sharp on different sized scales from the same fish. In other words, the shape and size of the scale can alter the original appearance of the rings. In looking at scales from the same fish, as in Figures 5c and 5d, a big difference in their shape and size can be seen, as also in Figures 5e and 5f. This difference in size and shape is reflected in the difference in the appearance of the rings. The effect of different scale dimensions, that is the asymmetry of the scale, on the appearance of the ring within one scale is also shown in Figure 6b.

When the rings were examined, especially the diffuse rings, they appeared to be compound as though they were made up of a number of rings in close juxtaposition. For instance in Figure 6c the third annual ring appears compound at the side of the scale. In various other scales it is possible to find traces of this compound nature in many of the diffuse rings.

The occurrence of rings which are double on certain of the scales taken from one fish, the doubling of the rings on asymmetric scales for part of their length only, the doubling of rings on the apex and the appearance of the diffuse rings suggest a fusion of rings, both accessory and annual, as a consequence of the reduced dimensions in the growth zones.

SCHNEIDER (1910) also postulated that fusion of the rings was possible. His original statement about this fusion is as follows: "Es können bei kleinen Schuppen zwei oder mehr Ringe verschmelzen die bei grösseren Schuppen desselben Exemplares deutlich zu unterscheiden sind". In SCHNEIDER's opinion also, the cause of the fusion of the rings was a reduction in the size of the growth zones. The same idea is expressed in one of his other statements: "Bisweilen sieht man ferner, dass bei unsymetrischen Schuppen auf der einen Seite zwei Ringe zusammenfliessen, die in der anderen Hälfte der Schuppe getrennt sind".

If the fusion of the rings on some scales from the same fish is due to the reduced dimensions of the scale and if the fusion of the rings on one part of the asymmetric scale is a consequence of the smaller dimensions of that part, there is really no reason why such a fusion would not take place during the life of the fish due to a reduction in growth. The rough coincidence of the disappearance of the paired rings with a big decrease in growth found in the scales of East Anglian herring favours the assumption of a fusion of rings following a reduction in the size of the growth zone. Also in favour of this assumption is the fact that the compound diffuse type of rings appears more frequently in the older fish, that is, in rings after the third. So, we can assume that two close rings appearing later in life after a big reduction in growth have to be taken as the annual ones.

An additional argument for the hypothesis that the fusion of rings follows a reduction in growth is the bigger number of paired rings on the scales of specimens showing a more uniform growth.

If it is accepted that a decrease in the size of the growth zones affects the appearance of the annual rings by causing fusion of the accessory with it, the corollary should also be true. This is, that if a wide growth zone follows a narrow zone, an accessory ring may reappear in association with a ring which has been preceded by a diffuse ring of an obviously compound type formed as a result of a narrow growth zone. In Figures 6d and 6e are shown examples of a dissociation of the rings.

So far, the fusion of an annual ring with an accessory has been dealt with. However, we had the impression that fusion of two accessory rings could also take place.

Annual Rings in the East Anglian Herring

In the course of our work it was noticed that both wide and narrow rings occur in the East Anglian herring. Both types could also be found in the same fish, as was mentioned. When a small scale showed a diffuse ring, a double ring would often be found in the same position on a large scale from the same fish. If a narrow ring appears on a small scale, the large scale from the same fish will often show a diffuse ring. When occurring as the first annual ring the compound nature seemed to be due to a closely associated accessory ring. In favour of this assumption is the fact that in the cases of asymmetric first growth zone it was sometimes possible to find on one side a rather diffuse zone, while on the other, two rings occurred. However, the first annual ring was often narrow.

The number of compound diffuse rings seemed to be frequent in the older fish and it has been assumed that this was due to one or more accessory rings occurring in the growth zone before the last one, at such a distance from the annual ring, that in the last growth zone a fusion of annual ring with the accessory took place. It was sometimes quite easy to classify the ring as compound, but on other occasions it was difficult to say whether a diffuse ring was compound or not. We cannot say definitely whether diffuse rings in the East Anglian herring were simple at all. Even for the sharp rings appearing on the small scales we suspect a compound origin. It could be assumed, however, that the frequent occurrence of wide diffuse rings in the East Anglian herring was mainly due to fusion of an accessory ring with an annual ring.

Summary

1. An attempt was made to analyse the appearance of the annual rings in the southern North Sea herring with a view to possible use in the separation of the various stocks of fish. In this work considerable difficulties were encountered, due to factors altering the appearance of annual rings.

2. Fusion of the annual rings with the accessory ones following a reduction in growth results in the appearance of compound diffuse rings. This fusion also occurs on scales taken from a different part of the fish due to the difference in shape and size of the scales.

3. The accessory rings are discussed in some detail because of their influence on the appearance of annual rings and their frequency on Southern North Sea scales. Considerably more work is needed for a full explanation of the origin of the accessories and the cause and result of their fusion with annual rings.

4. In view of the various factors which, it has been suggested, alter the appearance of the ring, it would appear that the ring type as a racial characteristic is rarely of use and the method is of no use in separating individual fish taken from similar environments.

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On the Behaviour of Elvers (*Anguilla vulgaris* Turt.) Migrating from the Sea into Fresh Water

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Introduction

Due to the steady demands to keep the inland waters of the low-lying parts of the Netherlands as fresh as possible, more and more dams, locks, and sluices are built as a separation between the sea and the inland water system. Hence elvers encounter steadily increasing difficulties to reach the inland waters from the sea and at some places it is even impossible for them to cross these barriers.

It was therefore decided to investigate the possibility to facilitate the inward elver migration, especially at the Afsluitdijk, which bars the IJsselmeer from the sea. In this respect it may be stated, that the most obvious solution of this problem, a so-called elver ladder, is practically impossible because these ladders would be immediately destroyed by heavy waves pounding on the dam. In order to reach a solution the need was realized to obtain some fundamental knowledge about the elver behaviour in the transition area between sea and inland waters, and on the factors influencing it. A series of observations was therefore carried out at the Afsluitdijk, the results of which are recorded here.

Observations

In the Netherlands most of the elvers normally arrive at about the middle of March (DEELDER, 1952), after cold winters later, after mild winters earlier. For a reason still unknown they assemble in front of freshwater outlets, such as sluice basins and estuaries, and stay there till their migration begins. During this period they are mainly active at night and during daylight hours they bury in the bottom or they swim in deep water (DEELDER, 1952). Therefore, practically all the field observations mentioned in this paper were made at night.

When one regularly observes the assembled elvers, differences are noticed

between the behaviour of those just arrived from the sea and those which are prepared to migrate into fresh water. These differences are linked by a gradual transition. These behaviour changes concern many items, such as vertical movements, schooling behaviour and reactions towards flowing fresh water, lamplight, area of orientation, and inward migration.

For a better understanding we will discuss some of the obvious characteristics separately; however, for practical reasons we will treat the vertical movements together with the schooling behaviour.

(a) Vertical movements and schooling behaviour

Shortly after their arrival no elver can be seen at the surface for several days. Experiments, carried out in a big aquarium containing about 20 m^3 of water, showed that in this stage the elvers swim individually, rather equally dispersed through the water layers, without any tendency to flock together or to congregate near underwater objects, such as banks.

Then, some days later, individual elvers may be seen for short periods near the surface. In the next days the number of elvers visible increases, together with the duration of their stay at the surface. In the meantime they appear to develop a tendency to congregate, this also in contrast to their former behaviour. The most striking phenomenon in this area is when great numbers of elvers swim in perfect harmony for hours along the walls of locks and sluices, using these as guides. It is an impressive sight to see a vast school of elvers swimming along a bank and then for some reason or other turning to open water and subsequently disappear. Or to see how two schools of elvers swim along a bank in opposite direction so that they meet each other and both of them just keeping on as if nothing happens and then parting again as if the elvers are completely ignored by those of the other school, swimming in the opposite direction. As will be discussed below, this phenomenon occurs often after a discharge of fresh water from the sluices or locks. In this connexion a fact well known in the inland waters may be remembered, where huge shoals of elvers are observed, migrating for days together along the banks of rivers or canals.

The orientation of elver shoals, either in the sea or in fresh water, may be mentioned here too. This is truly a remarkable phenomenon. Although in daytime elvers presumably use a visual orientation to keep themselves swimming parallel to walls or to dodge objects floating in the water, they also manage to do so in complete darkness, even when they swim at some distance from the solid objects, as may be observed when lighting a lamp for short periods or photographing them with a flashlight. Perhaps they manage to do so with the aid of their lateral line sense organ (DIJKGRAAF, 1947).

A rather easy method to determine whether or not an elver has already completed its behaviour change is to shine a strong light beam on it when it swims at the surface. The less an elver has changed, the quicker it dives down and becomes invisible. It is true that such elvers are attracted by light, but this only when the latter is very faint. They then congregate near the light, but stay well below the surface. Elver catchers, such as those operating in the river Severn, take advantage of this by illuminating the water near their catch instrument with a candlelight or faint kerosene lamp.

Elvers which have changed sufficiently and swim at the surface are, on the

contrary, not disturbed by a light, even when it is strong. They are always attracted by it. These observations render the elver migration in the rivers in broad daylight comprehensible.

(b) Reaction towards fresh water

Newly arrived elvers show no tendency to migrate into fresh water, they even try to escape when they get in it. At this stage, many elvers are killed by water pumps when they have accidentally got into fresh water, as they deliberately swim with the flow into the pump-inlets in their effort to escape. This behaviour contrasts sharply to the well known tendency, developed later, urging the elvers to swim against freshwater flows, and even encouraging them to leave the water and to climb against small tricklets, so that man may turn this to his advantage and build elver ladders enabling them to surmount barriers.

Attention must be drawn to the fact that this change in behaviour is also a gradual one and in close correspondence with that mentioned above. So it may, for instance, happen during the change-over that a discharge of fresh water into the sea results in the rise of numerous elvers towards the surface which formerly did not take place. The elvers then swim against the current, if it is not too strong, towards the sluice, where they assemble near the walls, and form shoals for a shorter or longer period. On occasions like these one perceives the first indications of a directed elver migration; as has already been mentioned, these indications become more and more distinct as the season advances.

As our observations are all of a rather subjective character we wanted to corroborate them by collecting data of a more exact nature. For this reason we carried out some experiments by which the change in behaviour could be put down in exact figures. In these experiments we studied the elver's reaction towards flowing fresh water.

The first series of experiments was carried out with use of a 6 litre aquarium. Two tubes served as inlet and outlet respectively so that a constant flow of fresh water passed through the aquarium in which the water level was kept constant. During the whole season this arrangement and the environmental conditions were kept as constant as possible, so that results obtained on occasions would be comparable.

The procedure was to put into the aquarium a number of elvers, usually some 30–40, freshly caught in the sea with the aid of a dip-net and handled with utmost care. After 15 minutes a count was made of the number that had stayed in the aquarium and of those that had left with the outflowing water. During these experiments the elvers showed very clearly the change in behaviour during the course of time. In the beginning of a season all the elvers immediately swam actively with the current to leave the aquarium through the outlet, head first. In a few seconds all the elvers had disappeared. At the end of the season the situation is reversed: then all elvers flock towards the inlet and try to swim upstream. If one of them is accidentally sucked in by the outlet, it wriggles and tries as best it can to get out of it. If it does not succeed, it is invariably sucked along tail first, still trying to swim against the current, but always in vain owing to the narrowness of the tube. Between these two extremes all types of graduation may be observed; for example, some of the elvers are swimming to the inlet while the others leave with the outgoing current. Or elvers may swim first to the inlet and then turn to be dragged passively by the stream, presumably

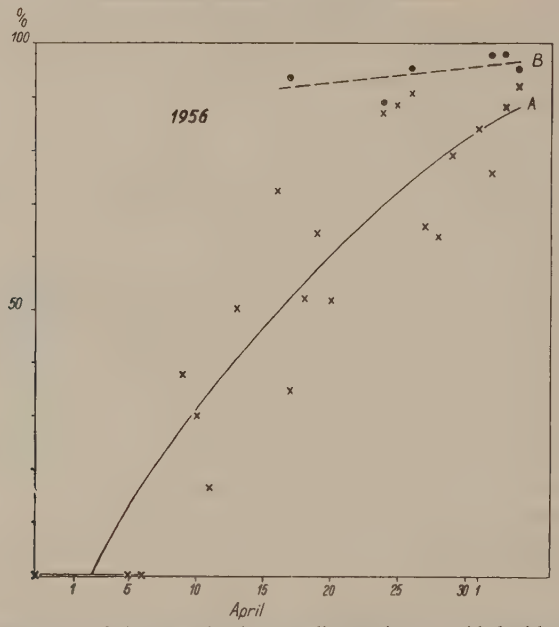

Figure 1. Percentages of elvers staying in a small aquarium provided with a constant flow of fresh water. The A graph refers to elvers freshly caught in sea at the sluices. The B graph refers to elvers caught while climbing against a freshwater tricklet.

because their migration urge is not yet strong enough and has rapidly declined by swimming upstream.

A good idea of this change in behaviour is obtained when one compares the percentages of elvers staying in the aquarium during the whole experimental series, as shown in Figure 1, graph A. When one examines this figure, one must remember that it refers to elvers freshly caught in the sea. So these catches consisted of individuals which may have been in front of the sluices for a different length of time.

In order to show again a change in behaviour and that there may be a given moment two physiologically different types of elvers in the same water, we carried out the same set of experiments with elvers which had been caught swimming against a freshwater tricklet near the sluices. As had been anticipated all these elvers showed, in the aquarium, a strong tendency to swim upstream. This is shown in graph B of Figure 1. The difference between graphs A and B is statistically significant ($t = 6{\cdot}4$; $p < 0{\cdot}01$). One should expect that the graph B would reach with the 100% line, but it does not. In our opinion this is because the elvers had used up so much energy in their efforts to climb against the tricklet prior to being caught that some individuals are not willing to swim upstream again.

Anyhow the difference between the graphs and the gradual change of graph A demonstrates very clearly that elvers change their behaviour after arrival at the sluices. The results obtained from other experiments are in agreement with

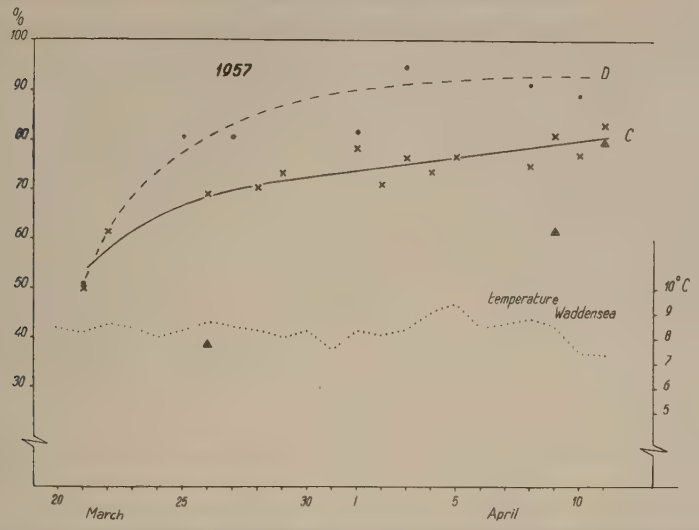

Figure 2. Percentages of elvers swimming upstream in a big aquarium provided with a constant flow of fresh water. The C graph refers to elvers freshly caught in sea at the sluices. The D graph refers to elvers caught at the beginning of the season and temporarily stored in a perforated box, floating in sea water. △ △: elvers caught far out at sea. Note the temperature of the sea water, which remained at a rather constant level.

this conclusion. These were carried out on a much larger scale, using a big aquarium, 15 m long, 0·8 m wide, and 1·8 m deep, which could be divided into four compartments by three vertical hatches. The water level was controlled by an overflow at one end, while at the other end fresh water could be pumped in at different rates. During the experiments the hatches were lowered down to 5 cm from the bottom and the amount of fresh water pumped in was thus regulated so that there was a constant flow along the bottom of 7 cm/sec. Freshly caught elvers were then liberated in the middle of the aquarium, usually some 200–400 of them. Half an hour later the pump was stopped, the hatches quickly closed and the number of elvers in each compartment counted. The difference between these experiments and those discussed earlier is, apart from the size of the aquaria, that here elvers could freely swim against the current and that they could not unwillingly be dragged by the flow, as was the case when they had been sucked into the outlet tube.

At first we invariably worked with freshly caught elvers. The results of these experiments are shown in Figure 2, graph C, which shows the percentages of elvers which actually swam upstream. In this graph the obvious absence of a group of elvers all of which failed to swim upstream has to be explained. In our opinion it is caused by the exceptionally heavy and continuous discharge of fresh water from the IJsselmeer in that particular season. As a result of this the water in front of the harbour sluices was presumably the same as the harbour water itself. Hence we might expect that elvers would stop their migration well in front of the harbour, instead of inside it, and consequently only came in when they had already, at least partly, changed their behaviour. It is anyhow

remarkable, that in the days preceding the experiments practically no elvers could be caught at the sluice, while Mr. CREUTZBERG of the Zoological Station at Den Helder made big catches just outside the harbour.

However, during the season we did manage to keep alive a number of elvers stored in a perforated box lying near the sluices in the very same water where the other elvers were freshly caught each time. The results of the experiments made with these elvers are shown in graph D of Figure 2.

There is an obvious difference between the two graphs, which in our opinion can only be explained by assuming that many elvers change their behaviour pattern during their stay at the sluices. In this way the percentage of elvers swimming upstream in the C series is, just like those of the A series of Figure 1, inevitably lowered because "new" elvers arrive constantly, and because some of those which did already change their behaviour managed to disappear in the IJsselmeer and so escaped being caught. This in contrast to the elvers of the D graph, which were the same individuals throughout the trial series.

The results may be summarized as follows. Field observations led to the supposition that elvers change their behaviour when they stay near the sluices before they migrate into the fresh water. Experiments were therefore carried out whose results lead to the conclusion that elvers do change their behaviour. Thus the field observations have been confirmed by experiment.

From our observations and experiments we strongly got the impression that for some reason or other elvers start their change in behaviour after their arrival in the vicinity of the sluices. We have already discussed the slower rise of the A and C curves, compared with the B and D curves, and explained it by assuming that new elvers arrived every day, even if in a steadily diminishing number, although a second explanation could be, that of the elvers arriving in the course of the season more and more have started their change of behaviour at an earlier phase. We also drew the attention to the relatively high percentage at which graph C started, which could also be explained in a plausible way.

However, there are still more indications which can be used to support our conclusions. These are obtained by three trials with elvers caught at sea by Mr. CREUTZBERG and kindly placed at our disposal. As these elvers were absolutely healthy and lively, we may use the results obtained despite the long journey before they could be put into the aquarium. These three results (Fig. 2) strongly suggest, that at least in the beginning of the season, the majority of elvers start their change in behaviour in the vicinity of the sluices.

(c) Migration and the depth at which the elvers swim

Up till now the depth at which the migration and orientation occur towards flowing fresh water has not been discussed. This changes too. Contrary to the common belief, the surface is not the only region in which an elver is able to orientate itself towards fresh water. It may do so just as well, possibly even by preference, in the deeper water, even close to the bottom. In this respect the experiments with the big elver aquarium were especially illustrative.

When an aquarium hatch separated a salt-water from a freshwater compartment and the water level in the latter was higher, by about 5 cm, we obtained freshwater leakages under the hatch as well as at the sides of it. This experiment was repeated many times in the course of the season and thus we could observe, that at the time the elvers began to react to such a freshwater stimulation, they invariably did this near the bottom. In the course of the

season these reactions became stronger and stronger, so that one could produce a genuine directed elver migration along the bottom into the freshwater compartment by just slightly raising the hatch.

In this stage, however, no migratory activity can be observed in the surface layer. This occurs later on in the season. We then observe the simultaneous orientation on seepage of fresh water in both the surface and bottom layers. In a still later phase we have reasons to assume that the elvers have fully switched over to migration in the surface layers. At the Afsluitdijk we were not in a position to investigate this phase, due to absence of elvers in this particular stage, those having already disappeared into the lake. I had, however, the opportunity to observe elvers migrating in the river Meuse at Lith, about 120 km upstream from the sea. Here an underwater observation chamber has been built along a newly erected fish-pass. Many times elvers have been observed and they invariably swam in the surface layer.

(d) Orientation

We have mentioned several times the orientation of elvers towards fresh water when this is flowing into sea water. With the use of coloured water we have been able to examine some characteristics of this phenomenon in greater detail. The impression was gained that if elvers are to orientate properly to a freshwater flow there must be a sufficient drop in salinity and a certain amount of turbulence caused by the inflowing fresh water.

With regard to salinity, Van Heusden (1943) examined the behaviour of elvers during extensive laboratory experiments, and concluded that a decrease in salinity has a stimulating effect upon elver migration proportional to the value of the decrease. These results are in full agreement with the well known behaviour of elvers in open water. Provided their behaviour has sufficiently changed, they show a strong interest in fresh water, even when it does not flow. When, for instance, a bucket with fresh water is lowered just under the sea surface, amidst elvers swimming at the surface, they at once get activated as soon as they reach the area of floating fresh water. This "activation" can be seen from the greatly increased swimming speed of the elvers, which cross the area at random.

A sluice discharging fresh water immediately induces many elvers to rise towards the surface where, if the flow is not too strong, they start to swim upstream, in the direction of the sluices. And we observed that when elvers climb out of the water against a freshwater tricklet they immediately turn when the tricklet is changed into a salt one. We have not investigated just how much the salinity has to be lowered before a response of elvers is obtained, but in our opinion this depends greatly on the advancement of the change in behaviour.

Besides the salinity differences we mentioned water turbulence as being necessary for a good orientation. Some experiments have been carried out on this factor. Due to the huge numbers of elvers in the open water, it was not possible to collect numerical data on this subject, but the fact that the elvers always react in the same way without even a single deviation strongly supports our experimental conclusion.

With coloured water it was demonstrated that fresh water, flowing into the sea without causing turbulence, increased the activity of elvers, but there was no sign of any directed movement towards the point where the fresh water

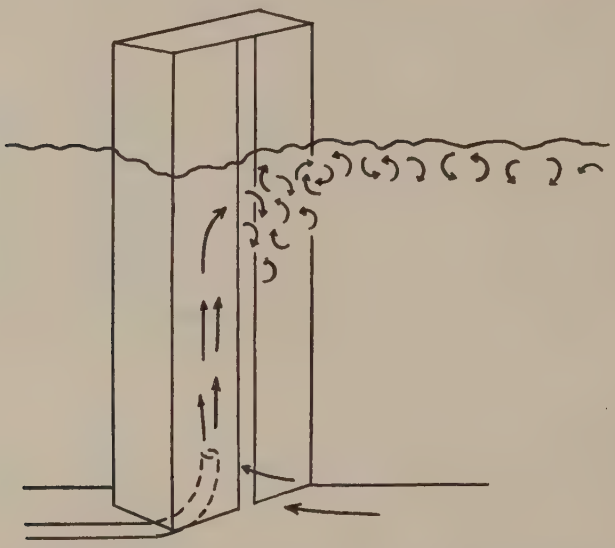

Figure 3. When an oblong box with a gap in one of its long sides is put upright in the sea and fresh water is pumped in at the bottom, sea water will be sucked in through the lower end of the gap and brackish water will leave the box through the gap near the surface, causing much turbulence. This situation is ideal to attract elvers which swim straight to the gap using the turbulence as a means for orientation.

entered. When, on the other hand, the fresh water entered in such a way to cause turbulence, without of course changing either the quantity or the quality of the fresh water, the same elvers swam at once straight towards the outlet. When changing the inflow again into a non-turbulent one, all elvers were at once disorientated, but immediately became orientated again when the turbulence was restored. This could be repeated over and over again.

It might be of interest to say that we prevented turbulence by using a plate over which the fresh water had to flow obliquely into the sea. It is also possible to prevent turbulence by keeping the freshwater influx tube horizontal. However, when we put an oblong box upright in the sea, with a gap in one of its sides as shown in Figure 3, and the pump outlet coming in at the underside, turbulence is created on a large scale by the brackish water which leaves the box at the sea surface.

The ability of elvers to locate the places where turbulence originates is in agreement with the view of DIJKGRAAF (1947), who examined the behaviour of fishes in the laboratory and concluded that such a location is achieved with aid of the lateral line sense organ which detects rises of pressure in the water and also the place where they spring from.

A situation in which superficial turbulence is produced on a large scale often occurs at the sides of sluice hatches and lock doors. Here the approach of thousands of elvers swimming in radial direction towards the leak has often been observed very clearly (Fig. 4). The elvers disappear continually through the leak but are steadily replaced by others. However, no elvers were to be seen

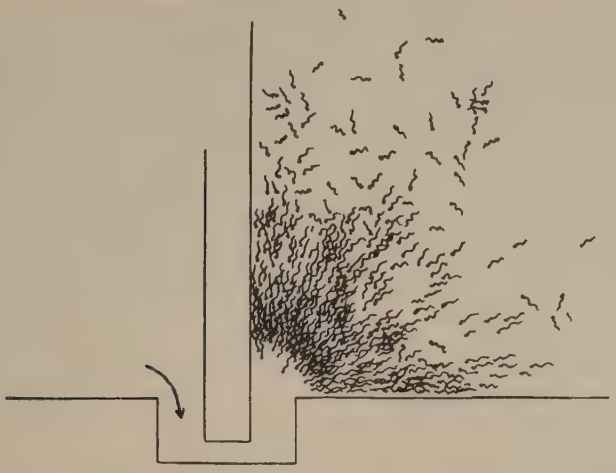

Figure 4. A diagram to show the radial swimming of elvers at the sea surface towards a freshwater outlet (along a sluice hatch) which causes equally dispersed turbulence along the surface. As soon as the turbulence ceases in a given sector (e.g., by wind influence), the directed migration of elvers in that sector stops immediately. Note the total absence of elvers in the surface layers at some distance from the outlet.

swimming on the surface more than a few metres away from the leak. Hence we tend to assume that elvers swim at some distance under the surface in the vicinity of the leak, then rise to the surface and continue there the migration straight towards it. This would imply a rough orientation under water first, followed by a more exact orientation at the surface. Unfortunately no detailed data could be collected about this phenomenon as it is impossible to see what happens at some depth under the surface of the water or to copy the situation in our elver aquarium, which is too small for this type of experiment.

We tried to examine the ability of elvers to orientate themselves towards underwater turbulence. This was done by closing a hatch in the elver aquarium but for a narrow gap at the bottom. As usual the hatch separated a freshwater compartment from one filled with sea water. When the freshwater level is raised sufficiently above the salt-water level, fresh water passes under the hatch into the sea water. If this pressure head is small, the fresh water immediately wells up to the surface along the saline side of the hatch without any sign of turbulence. But when the pressure head is greater, fresh water is pressed into the sea-water compartment in a horizontal direction. In this situation turbulence occurs, as was demonstrated with coloured water. In the first situation no elver succeeded in finding the freshwater leak, although they showed the well known response of increased activity, swimming at random along the surface and up and down along the hatch when they touched the freshwater area, which was welling upward and spreading along the surface. Only the elvers which arrived by chance at the gap tried to make their way through it. The behaviour of elvers which swam at the surface at the place where the fresh water welled up was very strange. (It should be borne in mind that only elvers which show an advanced change in behaviour tend to swim along the surface.) These elvers

continually raised their heads out of the water and tried to climb the hatch and aquarium walls above the water, notwithstanding these parts were dry and the fresh water came from below. This again is a clear proof of the elvers' incapacity to find a freshwater leak when there is no turbulence. The phenomenon has also been observed in open water (cf., VAN HEUSDEN, 1943).

The behaviour of the elvers was very different when the fresh water flowed more strongly underneath the hatch thus causing turbulence. Now the elvers were attracted even from a distance of several metres, and made their way straight to the gap and tried to get through it against the flow. Now there was no swimming at random, in fact it was a clear case of directed migration. When the gap was so wide that elvers could pass it and the flow diminished sufficiently, as a consequence of the gradual lowering of the freshwater level, the elvers shot through it at top speed. It was strange to note, that they did not stop, once they had arrived in the fresh water but kept on swimming in the same direction until they reached the very end of the freshwater compartment.

These experiments have been carried out in an aquarium with a depth of about 1 m but in our opinion this limited depth is not essential to this elver behaviour; hence we conclude, contrary to the common opinion, that elvers are able to orientate themselves towards fresh water not only at the surface, but also in deeper water, provided that in both cases the fresh water flowing in causes sufficient turbulence.

Discussion

From the foregoing we have learned that elvers do not immediately continue their migration after approaching fresh water. At first they evidently are repelled by the fresh water. Consequently they stay sometime in front of the freshwater area and it would be interesting to know how far away from the transition area the elvers stop their migration. I stated earlier (DEELDER, 1952) after studying the elver behaviour in the Waddensea in the vicinity of freshwater outlets, that no effect on elver migration could be traced to the direction of the tidal current. CREUTZBERG (1958) who studied elver movements farther out at sea stated, however, that a distinct relation does exist between tidal movement and elver migration, in such a way that the elvers are carried towards the land on the flood tide and bury themselves during the ebb. When fishing near the freshwater outlets CREUTZBERG had, however, the same results as I.

From these apparently contradicting statements we are forced to draw the only conclusion possible, that the elvers begin to change their behaviour at sea so that they are not carried right into the freshwater area by the flood tide. In 1957 this interruption of the passive migration had a striking result. We already mentioned the exceptionally heavy freshwater discharges in the spring of that year which resulted in a low salinity of the sea water in the vicinity of the sluices. The result was that the elvers stayed a long time in the transition area so that consequently huge concentrations were observed here, while there was an obvious lack of elvers nearer to the sluices. When the elvers finally arrived at the sluices it turned out that many of them had already made a complete change in behaviour pattern and were willing to migrate into the lake without any delay.

We can also give a plausible explanation of elver behaviour in tidal estuaries and rivers and of the fishing for them. As I had the opportunity to visit Epney

at the river Severn near Gloucester during 10 days in the spring of the year 1955, I can discuss the situation in this river as an example.

From our observations discussed earlier we assume that the elvers, after their arrival at the mouth of the Severn estuary from the Atlantic Ocean, will stop their migration for several days before they develop the tendency to continue their journey upriver.

During their stay in the mouth of the estuary the elvers will swim predominantly at random in the dark hours of the night. Hence we must assume, that the elvers swimming at night will be carried upstream by a running flood tide. After the flood tide has died away the elvers will be carried downstream again on the ebb. They probably will not yet stay upriver, because of their dislike to flowing fresh water. A strong indication that this view is correct is the total absence of migrating elvers in the various brooklets running into the river. I presume that in this period the elvers move upstream and downstream in the river mouth, carried by the tide. The distance that the elvers are carried upstream depends on the strength of the flood tide and as this is expressed in height of the highest water level there exists a direct relation between water level height and upstream elver movement. (The relation between elver fishing and moon phases alleged at some rivers, as in the Loire, is in our opinion only of an indirect nature, for it is the moon which influences the tides and their height, and thus influences the elver movements.) The Severn flood tides which reach Epney reach a height of about 20–24 ft. at Sharpness. Tides with such a height will allow elver fishing at Epney. Higher tides will carry the elvers still further upstream; on the lower tides the elvers will not come as far as Epney. That elver fishing is particularly carried out at Epney is, in my opinion, due to the fact that the river-bank is very accessible here as there is a road running along it.

When the elvers have changed their behaviour sufficiently, we must assume that they are more and more inclined to stay at the places where the flood tide has carried them and will continue their own active migration upriver. I believe that elvers may easily be carried beyond Epney, so that very few elvers migrating at the surface are observed, this in contrast to places further upstream, such as Tewkesbury, where big elver shoals are sometimes reported.

With regard to the elver fishing at Epney, of which the description of Fisher and Lübbert (1908) still holds good, the following remarks can be added. The fishermen each have their own individual style of fishing, which every one claims to be the best. Some keep their scoops upstream to "catch the downstream moving elvers", some keep their scoops downstream to "enable the upstream swimming elvers in reaching an area of less flowing water", while others again move their scoop constantly through the water. But although their methods of fishing differ completely, there is one feature they all have in common, that is a faint lamp illuminating the nearby water surface. And, in my opinion, it is this lamp which ensures the success of the fishing as we know that elvers in this particular stage of behaviour tend to approach a faint light, so that an elver concentration is brought about which makes fishing profitable.

This description only applies to fishing at night. I was told, however, that fishing in daylight may occur occasionally. This could be explained in terms of very turbid water which induces elvers to keep swimming and subsequently be carried upstream, while the elvers should moreover occur in such great numbers that a concentration along the river-bank is not necessary to make profitable fishing.

Summary

1. Field observations and experiments revealed that elvers arriving out of sea in front of freshwater areas stay there for several days, during which period they considerably change their behaviour.

2. One of the most pronounced changes is in their response towards flowing fresh water. At first elvers are repelled by it, later attracted.

3. Other obvious changes occur in their schooling behaviour, the tendency to swim at a given depth, and their reaction towards lamplight.

4. It has been discovered that a direct orientation towards a freshwater outlet follows when considerable turbulence is created by the inflowing fresh water.

5. A tentative explanation is offered of the vicissitudes of elvers in tidal estuaries.

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Some Seasonal Variations in the Catch and Stock Composition of the Lobster

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1. Introduction

Assessment of the need for conservation and the particular measures to be adopted rest mainly on a consideration of the stock compositions. Consequently, it is important to know the seasonal variations which occur in order to arrive at a true estimate of the overall composition of the stock and, if practicable, to take advantage of recurring seasonal variations in devising suitable legislation. The Interdepartmental Committee on Crabs and Lobsters in their Report on Lobsters (1926), describe certain seasonal variations occurring in lobster stocks around the British coasts. In view of the bearing of this subject on the essential task of estimating lobster populations, a fuller investigation, relating the seasonal variations in the stock composition to a variety of size groups, was undertaken at the Marine Laboratory, Aberdeen.

2. Material and Methods

During the years 1932 to 1938 inclusive, commercial creel fishermen — one at Rousay, Orkney, and another at Burnmouth, Berwickshire — were commissioned to measure, throughout the season, a sample of about two thousand lobsters, to record the measurements to the nearest quarter of an inch and to classify the samples into males, berried females, and non-berried females. Certain aspects of these data have previously been reported (Thomas, 1951, 1955). Lobsters were measured from the tip of the rostrum to the end of the telson with the abdomen fully extended. They have here been classed into one inch length groups: for example, the 9 in. group embraces all lobsters of 9 in. and over but of less than 10 in. in length.

In 1949 and 1950 respectively, similar observations were obtained but, in addition, the catch was related to effort, measured in terms of the number of creel hauls. Also, the total number of lobsters and crabs landed and the corresponding effort were obtained monthly in respect of Burnmouth for the years 1950 to 1953 inclusive. Data on the numbers and weights of lobsters marketed

have been supplied by merchants in Orkney. The creeks of Rousay and Burnmouth have been chosen for this investigation as representative of, in the former case, a moderately exploited stock devoted exclusively to the capture of lobsters and, at Burnmouth, a heavily fished area from which both lobsters and crabs are landed. The overall annual mortality among the marketable stock of lobsters at Rousay may be taken roughly as 30%, compared with about 70% at Burnmouth (Thomas, 1955).

3. Fishing Practice and Landings

The fishery at Rousay is carried out at all seasons, though with different intensity. It is undertaken by small craft, mostly fishing grounds adjacent to the moorings, although there is some tendency to range farther afield during the period of long daylight and good weather. The latter factor is not, however, of great significance since the Orkney group of islands form a circle and, in the case of Rousay, the fishing grounds are well sheltered and can be worked at all seasons. The tendency to range farther afield on longer days is also limited in its effect because at such times other craft, principally from the mainland, are extending their range and crowding the local boats on to their "own" ground. The Rousay data therefore relate in large measure to a single local, moderately exploited, stock of lobsters which is fished throughout the year.

The landings of lobsters related to fishing effort are given in Table 1. Landings are heavier in the period May to November, reaching a peak in September, when also the catch per unit effort is highest; the latter fact may, in part, be attributable to the method of working in that at this season the creels are shot close inshore and can be sited carefully so as to be most effective. To this extent and on account of the effect of temperature on the activity of the lobster, a creel haul does not constitute a uniform measure of fishing effort at all seasons. However, in addition to these factors, September is the post-moult period of main recruitment to the stock of marketable lobsters and this will also result in a seasonal increase in the catch per unit effort which, in this instance, is a true reflection of the more abundant stocks.

Because of the unknown seasonal variability in effort, relating the catch to creel hauls is not suited to a study of seasonal variation in the stocks of lobsters. In consequence, the present investigation has been based on a consideration of seasonal changes in relative *proportions* of the various classes of lobster.

Whilst, as has been stated, the lobster fishery at Rousay is characterized by the area of fishing being more or less uniformly exploited, it is probably exceptional in this respect. Commonly, a creel fishery has seasonal peculiarities in its methods. For instance, at Stromness, Orkney, during the longer days when also the weather is good, creel fishermen work more prolific grounds farther afield on the exposed shores of the islands, thereby resting the sheltered grounds near to base which are worked during less favourable weather. This is reflected in the size of lobster landed. The average weight of lobster landed at Stromness in 1951 and 1952 was 525 g, but with the commencement of fishing on the exposed grounds in March it immediately rose by 30% and this average was sustained (Table 2). A comparable change in fishing grounds does not occur at Rousay. There is nevertheless a seasonal variation in the size of lobsters landed (Table 1). This will be considered later in the section dealing with length distribution (p. 150).

Table 1

The landings of lobsters, the average size of lobster, and the catch per 100 creel hauls at Rousay, by months, averaged over the years 1949 and 1950

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Overall
No. landed '00s.....	6	4	4	5	15	18	15	25	30	23	15	8	168
Mean length	11·2	11·0	11·1	11·6	11·9	11·6	11·6	11·4	11·3	11·4	11·3	11·1	11·4
Catch/100 creel hauls	39	41	37	37	32	37	40	63	73	63	52	46	51

Table 2

The landings of lobsters and the average individual weight at Stromness, Orkney, by months, averaged over the years 1951 and 1952

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Overall
No. landed '00s.....	2	1	2	4	40	39	23	19	38	32	14	8	221
Mean weight, g.....	590	525	695	641	695	717	714	632	626	632	601	592	629

Table 3

The total landings and the catch per 100 creel hauls of lobsters and crabs, respectively, at Burnmouth, by months, averaged over the years 1950 to 1953 inclusive

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Overall
Lobsters													
No. landed '00s.....	19	16	29	43	35	14	21	139	136	107	47	35	640
Catch/100 creel hauls	7·5	6·8	9·8	16·6	9·9	4·4	6·7	34·5	34·4	30·5	20·0	13·3	17·5
Crabs													
No. landed '00s.....	735	566	790	714	907	638	545	482	401	419	326	507	7029
Catch/100 creel hauls	296	242	264	277	257	203	171	120	102	119	140	194	192

In many areas creel fishing is devoted to the capture of both lobsters and crabs, and in such cases fishing methods may be varied seasonally, with the emphasis moving between these two species. Burnmouth is in such an area. Table 3 shows the landings of lobsters and crabs at Burnmouth related to fishing effort. During April and the months August to November inclusive, the fishery is directed mostly at the capture of lobsters, whilst in January, February, and March it is mainly centred on crab fishing. In other months the emphasis may vary according to the relative availability of the two species and the prevailing weather conditions. Crab fishing is undertaken in deeper water where both gear and operations are safer than on the shallower lobster grounds. As would be expected, heavy landings of lobsters are generally accompanied by a low level of crab landings and vice versa.

Whilst seasonal variation in the stock composition of lobsters will occur, in interpreting any data, especially those based on commercial fishing, due regard must be given to any seasonal variations in fishing practice such as the above.

4. Length Distribution

As the mature male lobster moults roughly twice as frequently as the mature female lobster, which in general casts about every other year, the length

Table 4

The size composition of male lobsters landed at Rousay expressed as a percentage of the total number of male lobsters of overall length 9″ and above in respect of certain length groups, by months, averaged over the years 1932–38 inclusive, and the average length of male lobster landed

Length	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Overall
9″	20	23	23	16	13	14	14	17	22	19	22	21	18·9
10″	23	25	25	19	19	18	18	22	25	25	23	27	22·7
11″	23	23	19	22	22	18	21	18	22	22	21	22	21·3
12″	18	16	17	20	21	23	22	22	17	19	19	15	19·0
13″	10	8	10	14	15	14	15	12	9	9	10	10	11·2
14″ and over	6	5	6	8	10	13	10	9	4	6	5	5	7·0
Average length	11·4	11·3	11·3	11·7	11·9	11·9	11·9	11·7	11·3	11·4	11·4	11·3	11·5

Table 5

The size composition of female lobsters landed at Rousay expressed as a percentage of the total number of female lobsters of overall length 9″ and above in respect of certain length groups, by months, averaged over the years 1932–38 inclusive, and the average length of female lobster landed

Length	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Overall
9″	16	14	12	9	7	5	4	8	15	16	14	13	10·7
10″	28	24	27	18	15	15	17	19	31	28	28	29	22·7
11″	24	26	27	28	27	26	26	21	25	26	29	28	26·0
12″	15	17	18	27	24	26	23	24	16	15	18	18	20·5
13″	11	11	11	12	16	17	18	18	9	9	7	7	12·3
14″ and over	6	8	5	7	10	12	12	10	5	7	4	5	7·8
Average length	11·4	11·6	11·5	11·9	12·1	12·2	12·2	12·0	11·4	11·4	11·4	11·4	11·7

compositions of males and females will differ (THOMAS, 1955). They are therefore to be considered separately.

The length composition of male lobsters landed at Rousay is given in Table 4. The percentage of 9 in. lobsters in the catch is low in May, June, and July, being 12·8% in May as compared with 22·9% in February; the percentage of 10 in. lobsters is lowest in June and July; 11 in. lobsters in June and August. Offsetting this the percentage of larger lobsters is progressively smaller in the later months. The trend is for each successively higher size group to be at its minimum as a proportion of the catch at a progressively later time.

Prior to casting lobsters cease feeding and are not usually taken in creels for three weeks after casting, until the shell becomes hardened. The total period when they are not normally entering creels is roughly five to six weeks. Taking the stock as a whole, this coincides with the period of reduced catch per unit effort, namely May (Table 1). If the seasonal pattern of casting was roughly the same for all size groups the length composition of the stock would not be affected. The most reasonable interpretation of the observed variations in the size composition of the stock is that larger lobsters tend to cast progressively later in the year. On this basis the data suggest that 9 in. male lobsters at Rousay are mainly casting in May to July, 10 in. lobsters in June or July, 11 in. lobsters in July to August, and larger sizes in September or even later still.

There is a secondary decrease in the proportion of 9 in. lobsters in October (19·4 as compared with 22·2 and 21·8 in September and November, respectively);

Table 6

The size composition of male lobsters landed at Burnmouth, expressed as a percentage of the total number of male lobsters of overall length 8″ and above in respect of certain length groups, by months, averaged over the years 1932–38 inclusive, and the average length of male lobster landed

Length	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Overall
8″	10	10	10	17	11	14	16	15	15	12	17	14	13·6
9″	33	32	39	41	37	30	31	34	34	31	32	33	33·8
10″	34	31	31	23	29	28	29	28	26	30	26	29	28·5
11″	17	19	16	14	16	20	18	16	19	19	18	17	17·5
12″ and over	6	8	4	6	6	8	7	6	6	8	8	6	6·5
Average length	10·3	10·3	10·2	10·0	10·2	10·3	10·2	10·1	10·2	10·3	10·2	10·2	10·2

Table 7

The size composition of female lobsters landed at Burnmouth, expressed as a percentage of the total number of female lobsters of overall length 8″ and above in respect of certain length groups, by months, averaged over the years 1932–38 inclusive, and the average length of female lobster landed

Length	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Overall
8″	6	8	6	9	7	6	9	10	9	11	13	8	8·7
9″	18	16	16	17	19	17	19	23	23	23	18	17	19·0
10″	44	43	44	44	41	40	37	39	39	38	39	44	40·6
11″	24	26	27	24	26	28	28	23	25	23	22	25	25·0
12″ and over	8	6	7	7	8	9	8	6	4	6	7	6	6·7
Average length	10·6	10·6	10·6	10·5	10·6	10·7	10·6	10·4	10·4	10·4	10·4	10·5	10·5

similarly for 10 in. lobsters in November. This may well signify a second subsidiary casting season in these size groups. WILDER (1952) concludes from marking experiments that a proportion of lobsters (*H. americanus*) of between 8 and 10 in. in length cast twice in the year whilst in the case of larger male lobsters moulting is annual. The present data suggest similar characteristics for *H. vulgaris* at Rousay. The general interpretation is of a progressively longer inter-moult period as the size increases so that the larger lobsters of length 14 in. and over may well cast only every eighteen months or even two years.

In the case of female lobsters (Table 5) the same interpretation is applicable as with males. The 9 in. length group is at a minimum in June and July when this size is casting. The 10 in. lobsters on the average moult after about eleven months, in May and June. The peak casting season for 11 in. lobsters is in August and the 12 in. group in September/October, with larger lobsters moulting still later. It is noteworthy that the peak moulting season for females does not follow the same pattern in relation to size as for males. The significance of this in relation to sex ratio will be discussed later (p. 152).

The length distributions of male and female lobsters at Burnmouth are given in Tables 6 and 7, respectively. The area is one of intensive fishing for both lobsters and crabs (Table 3), and variation in the length composition of landings mainly reflect changes in the fishing grounds so that other influences are masked. The higher than average size of lobster in the catch during the early months of the year, which is accompanied by the seasonal lowest catch of lobsters per unit effort and the highest for crabs (Table 3), reflects the fact that the fishing, primarily for crabs, is being prosecuted on the offshore grounds. Effort switches

Table 8

The percentage of males to total lobsters at Rousay in respect of certain length groups, by months and overall, averaged over the years 1932–38 inclusive

Length	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Overall
9″	58	63	65	62	58	67	72	68	66	59	64	65	64
10″	46	50	49	48	51	47	47	54	51	51	49	52	50
11″	51	47	42	41	40	33	41	46	54	50	45	48	45
12″	56	50	49	39	41	39	44	47	58	60	54	49	48
13″	49	44	48	52	43	37	41	40	58	56	60	61	48
14″ and over	52	36	58	50	43	45	42	45	55	51	53	52	47
Overall	52	50	51	47	45	42	46	49	57	54	53	54	50

Table 9

The percentage of berried to total females at Rousay in respect of certain length groups, by months and overall, averaged over the years 1932–38 inclusive

Length	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Overall
10″	25	24	27	22	24	23	15	12	20	24	32	28	24
11″	51	46	44	48	54	47	48	27	37	45	50	49	46
12″	43	43	46	51	40	52	41	36	42	62	48	45	46
13″	37	36	44	47	42	40	43	44	48	66	55	46	44
14″ and over	32	33	52	51	39	40	39	35	52	69	50	24	41
Overall	32	32	35	41	39	41	37	28	29	39	39	35	36

to lobsters in March to May. During this period, as well as from August to December, the average size of lobster caught is less than that from the crab grounds. The decrease in lobster fishing during June and July is the result of a switch from this fishing, brought about by the low catch of lobsters on account of the incidence of the main casting season. As the stocks are so intensively fished, the marketable sizes are concentrated in the lengths immediately above the minimum legal size and, even though larger lobsters may cast at some other season, the stock taken as a whole is largely not available to the creel fishing from about the middle of May to the end of July.

The peaks in the proportion of 8 in. lobsters in the catch during April and November (Tables 6 and 7) are almost certainly due to recruitment from the 7 in. group, which is therefore casting twice in the year, in about February and September. The data also suggest that 9 in. lobsters, both male and female, are mainly casting around June. However, the difficulty of dissociating the seasonal variations in biological factors from changes in fishing methods precludes any detailed analyses.

5. Sex Ratio and Spawning

The effect of fishing intensity on the overall sex ratio and the proportion of females in berry has been discussed by THOMAS (1955). Within this pattern seasonal variations will occur if male lobsters of a particular size group differ from the similar sized females in their main casting season. The percentage of males to total lobsters landed at Rousay is given in Table 8. The proportion of males in the 9 in. group is at a maximum in July, of 10 in. in August, of 11 in. in September, and of 12 in. in October, suggesting that these months represent the peaks of the casting season for female lobsters in these length groups.

On the west coast of Scotland spawning begins in June, but is most intensive in September, whilst hatching begins in May (Interdepartmental Committee on Crabs and Lobsters, 1926). The same general pattern is apparent around Orkney where the proportion of berried to total females is at its lowest level in August (Table 9). On the other hand, whilst this is applicable taking the stock overall, since the majority of mature lobsters fall into the 10 in. to 12 in. length groups, it is notable that in the case of 12 in. lobsters the seasonal variation is less marked than in the case of the smaller size groups, and for still larger lobsters the pattern is different. Lobsters may spawn at any season, and with the onset of maturity the regular pattern of spawning around September arises. On the other hand, with increasing size and accompanying longer inter-moult period, but a constant incubation period of about ten months, the spawning season becomes less precise.

6. Discussion

It is not at present possible to determine the age of crustacea, and for this reason length analysis assumes an even greater importance than in most species of fish. Apart from tagging experiments, which involve considerable effort and which are subject to certain limitations, a comparison of the length composition of the stock in the light of a knowledge of growth-rates affords the only means of estimating mortalities. Seasonal variations in stock composition introduce a potential source of error. They appear to be of two kinds, (a) more or less regular ones, due to biological characteristics of all lobster stocks (e.g., recruiting, moulting, etc.) and (b) those which vary from place to place and are caused by differences in fishing habits, etc.

In these investigations seven years' measurements have been grouped together and it may well be that the true seasonal variation in any one year is greater than appears from the results. Certainly the casting season must be expected to vary slightly from one year to another. In consequence, year to year observations are not strictly comparable, even if taken in the same month, unless the season of sampling is carefully chosen. The difficulties, however, may not be as serious as results based on consideration of percentage composition suggest. The most variable group is that immediately above the minimum marketable size. Whilst variations in this class will affect the percentage composition of the stock, they need not be used in estimations of mortality rates, which can be based on the relative proportions of lobsters in the middle of the range caught by creels. In any case this is preferable because it lessens the effect of creel selectivity.

Careful selection of the season of sampling will overcome, to a considerable extent, the inaccuracies liable to arise from variations in fishing methods. However, in this case it is essential to distinguish between stocks. Lobsters are relatively stationary and in consequence it is usual to find different stock compositions and mortalities on the various grounds — for instance, inshore and offshore. For some purposes it seems desirable to treat these as separate stocks so that combination of data from regular monthly sampling cannot be adopted as a means of eliminating the effects of seasonal variation to get an overall estimate. Because of the very small amount of movement, investigations of lobster stocks, even more than with most species, demand an intimate knowledge of fishing practice.

7. Summary

1. Landings of lobsters vary seasonally, both in total number and in catch per unit effort.

2. The length compositions in a stock, both males and females, vary seasonally. This is attributable to a difference in the main casting season through the various length groups.

3. The sex ratio shows a seasonal variation, both overall and within different length groups. These factors result from a difference in the main casting seasons of male and female lobsters.

4. Spawning around Orkney is most intensive in September, whilst hatching occurs roughly ten months later. The seasonal pattern of spawning and hatching is better defined in newly matured lobsters than in older individuals.

5. Seasonal variations due to the biological characteristics of the stock are often masked by changes in the methods of fishing.

6. The significance of seasonal variations, both biological and in the fishing methods adopted, is discussed in relation to the estimation of stock compositions and mortality rates.

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Letter to the Editor

In addition to the critical remarks of SAELEN (1957) on KRAUSS' (1955) idea of a possible haline circulation in the Norwegian Sea, some attention should be given to the numerical values used in that paper.

1. The differential equation of a salinity disturbance originating from the coast requires the existence of a source of fresh water on the coast. This source is mathematically equivalent to a flow of salt towards the coast, which is assumed by the author to be $A = 31{\cdot}4 \times 10^{-3}$ g cm^{-2} sec^{-1}. This flow is not independent of depth, but it is assumed to decrease as cos ωz from the surface to 100 m depth. When integrating A cos ωz between 0 and 100 m, one obtains a flow of 200 g cm^{-1} sec ^{1} of salt towards the coast. At a salinity of 33·3 $^{0}/_{00}$ this value is equivalent to a flow of 6000 g cm^{-1} sec^{-1} of water from the coast into the sea or to a discharge of about 18×10^{10} g water per cm of coast line and per year. On a strip of land, 300 km wide, this amount would require a rainfall of 6000 cm, which is about 60 times the observed value. It is not stated in KRAUSS' paper how he obtains his value of A.

2. The coefficient of lateral eddy conductivity is taken as $\eta = 10^8$ g cm^{-1} sec^{-1}, but as more modern investigations have shown this coefficient would not be larger than 10^5 10^6 g cm^{-1} sec^{-1} (STOMMEL, 1955). This coefficient is about 100 times smaller than the value used by KRAUSS. However, the horizontal salinity gradients $\left(\frac{dS}{dx}\right)$, at least at the shore, would not be so much affected, because η and A are connected by the equation $\left(\eta \frac{dS}{dx}\right) x = 0 = A$ cos ωz, and both values are about 100 times too large. But the coefficient for the vertical eddy diffusivity of 10^2 g cm^{-1} sec^{-1} also seems to be rather high.

3. With these remarks and the corrections of the derived velocities given by KRAUSS which at their maximum are 10 cm/sec along the coast, it seems more than doubtful that this haline field could produce a real circulation in the whole Norwegian Sea. Moreover, the effect of the fresh water addition from land on the salinity near the coast is restricted to the top layer and does not affect the deeper layers, which according to the observations are involved in the circulation in the Norwegian Sea. On the other hand it cannot be denied, that the discharge of fresh water from the coasts of the Norwegian Sea will have an influence on its circulation at least close to the shore.

It should, however, be emphasized that numerical values applied to mathematical models should be more carefully considered, and that the sources of these values should be discussed in detail.

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Reviews

J. B. Tait. "Hydrography of the Faroe-Shetland Channel 1927–1952". Scottish Home Dept., Mar. Res., 1957 (2). Edinburgh, 1957.

In dem grundlegenden Buch "The Norwegian Sea" von HELLAND-HANSEN und NANSEN, wie auch bereits in den früheren Arbeiten, ist auf die grosse Bedeutung, welche die Faroe-Shetland Region für die gesamten Meeresgebiete nördlich Europas und Sibiriens hat, hingewiesen worden. Hier befindet sich der wesentlichste Durchlass warmen Atlantischen Wassers. Es entspricht der Bedeutung dieses Gebietes, dass in ihm seit über 50 Jahren systematische Untersuchungen durchgeführt werden.

J. P. JACOBSEN hat den ersten Teil des vorhandenen Beobachtungsmaterials (1902–1939) verwendet, um die Schwankungen im Volumentransport des Atlantischen Stromes zu berechnen. Danach ergaben sich Mengen zwischen minus 2·7 und plus 21·8 km^3/hr. Die grossen Differenzen allerdings, die zwischen zwei nur um ca. 50 sm. entfernten Profilen auftraten, machten es wahrscheinlich, dass die berechneten Werte durch unerwünschte Störungen (interne Wellen, Mangelhaftigkeit der dynamischen Methode usw.) beeinflusst waren, auf deren Existenz schon die früheren Untersuchungen von "Dana" und "Michael Sars" aus dem Jahre 1910 hingewiesen haben.

J. B. TAIT hat, nachdem den beiden Auszügen "Long-term trends and changes in the hydrography of the Faroe-Shetland Channel region" (Pap. Mar. Biol. and Oceanogr., Deep-Sea Res., Suppl. to 3) und "Recent oceanographical investigations in the Faroe-Shetland Channel" [Proc. roy. Soc. Edinburgh, Sect. A, **64**, Pt. 3 (18)] bereits vorläufige Ergebnisse zu entnehmen waren, nunmehr das Gesamtresultat der neuen Untersuchungen über die Schwankungen in diesem Raum vorgelegt. In zwei Abschnitten werden die Intensität des Atlantischen Stromes und die Wassermassen beschrieben. Besonders aufschlussreich ist das sowohl in Tabellenform als auch in der Verarbeitung als hydrographische Schnitte in 74 Abbildungen wiedergegebene Originalmaterial. Dies beschränkt sich allerdings auf die Jahre 1927–1952, da nach Ansicht des Verfassers besonders in den früheren Beobachtungen Störungen zu erwarten sind. Die textlichen Erläuterungen weisen auf viele Einzelheiten hin. Folgende Ergebnisse seien hervorgehoben: —

1. Die Intensität der Strömung schwankt langperiodisch; 1929 wird ein erstes Maximum, 1951 ein zweites erreicht. In den dreissiger Jahren ist die Strömung hingegen bedeutend schwächer. Der Unterschied zwischen den stärksten und schwächsten Volumentransport beträgt 21·2 km^3/hr.

2. Einschübe von Mittelmeerwasser sind in der Mitte der dreissiger Jahre besonders stark und verschwinden am Ende des Dezenniums.

3. Durch Mischung und Abgleiten entsteht in diesem Raum zeitweise ein neuer Wasserkörper mit Temperaturen unter 0° und sehr hohem Salzgehalt, welcher dann im Bodennähe gefunden wird. Auf diesen Vorgang lassen auch die Inversionen in der Dichteverteilung schliessen, welche relativ häufig auftreten.

Inwieweit dynamische Berechnungen in diesen nordischen Regionen absolute Geschwindigkeitswerte ergeben, wird sicherlich zur Zeit nicht einhellig entschieden werden können. Das vorgelegte und bearbeitete *direkte* Beobachtungsmaterial ist jedoch von einer so grossen Bedeutung, dass dieser Band von J. B. Tait heute die grundlegendste Abhandlung über die hydrographischen Verhältnisse in Faröer-Shetland-Kanal darstellt.

W. Krauss

V. Cviić. "Distribution of bacteria in the waters of the mid-Adriatic Sea". Inst. Oceanogr. Ribarst. Split, M. V. "Hvar" cruises, Res. Fish. Biol. Rep., **4** (1): 1–44, 13 figs. Split, 1955.

The paper presents the results of bacteriological investigations carried out in the Adriatic Sea in 1948 and in 1951–53. During these periods water samples from different depths were taken monthly at certain stations in the open mid-Adriatic and in coastal areas. The horizontal and vertical distribution of heterotrophic bacteria, as well as the diurnal and seasonal fluctuations, were examined, and the presence of some physiological groups (nitrate reducing, starch-hydrolizing, ammonia- and hydrogen sulphide-producing) was tested in selective media. Several strains were isolated and determined to species. Finally the fluctuations in the bacterial population were studied in relation to certain ecological factors viz., temperature, salinity, oxygen content, and amount of free phosphates.

The author distinguishes three zones in the horizontal distribution of bacteria, based on the average number of bacteria per millilitre in samples from four depths at each station. The most abundant bacterial population is found in a horseshoe-formed area influenced by supply of organic matter from soil and rivers. The area poorest in bacteria is the basin of Dubrovnik at the entrance to the Adriatic Sea. There is also a difference between the zones with respect to individual species. Predominant species from the two inner zones are lacking in the outer area, and vice versa. The vertical distribution of bacteria in the outer area shows little variation at different depths, while the open water of the mid-Adriatic has a distinct maximum at about 30 m. At the stations on the coast the number of bacteria increases from the surface to the deepest sample, which is at 60 m. In Table 4 the author has compiled results of quantitative bacterial examinations from other parts of the world. Most of the data quoted show an increase in the number of bacteria from the surface down to a certain depth, and then a decrease. An exception is the Clyde area studied by Lloyd (1930), who found, that not only in the locality cited, but at three other stations followed throughout a year, the maximum number occurred near the surface.

In chapter 4 the author discusses fluctuations in the bacterial flora. The diurnal variations show the maximum number of bacteria at greater depths at noon than during the morning and evening. However, the material is too small to allow final conclusions, and the investigations are continuing. The annual fluctuations have been examined at monthly intervals during two years.

The results are presented in a graph (Fig. 4) and a corresponding table. Based on samples from four depths ranging from 0 to 60 m, two maxima and two minima may be distinguished during the first year. In the observations from the second year there is a discrepancy between the table and the graph. While the table states 6 bacteria/ml at 60 m depth on the 15. July 1952, the graph shows 6,300 bacteria/ml. If the table is correct — and it probably is, because the following graphs are based on this number — the peak of the graph on this date should be changed to a minimum. As observations for the following three months are lacking, it is impossible to tell if there is a summer maximum this year or not.

In order to test the reliabilility of conclusions based on one single sample, the author made an experiment of great interest to all marine biologists. He collected samples from identical position and depth at 48 hours intervals, and examined the temperature, salinity, oxygen content, and number of bacteria. The material comprises repeated samples from four different depths at the same position, collected twice during winter and twice during summer. The results show that while the number of bacteria varies little at 0 m and 20 m depth, large fluctuations take place in deeper layers. At 40 m the largest difference was 16,000 bacteria/ml, at 60 m it was 15,300 bacteria/ml, while the minimum difference was 1 bacteria/ml. The author applies the average for the 4 depths, which reduces the 48 hours difference to about 4–6,000 bacteria/ml. It is, however, a question if in this case the actual numbers are not more characteristic — even if they are somewhat discouraging for cases where only single samples are accessible. They show that the bacterial population does not always follow the variations in hydrographical data. The author indicates that the varying number of bacteria in 60 m depth may be connected with the bacterial activity in dead phyto- and zooplankton, and this seems a reasonable explanation.

The physiological properties of the bacterial population indicate that proteolytic bacteria are very numerous in the Adriatic. A striking feature is that anaerobic sulphate-reducing bacteria are present in 63 per cent. of 100 water samples although the oxygen content as a rule is above 5 ml/l.

Among the ecological factors only the phosphate, and to some degree, the oxygen content, indicate a correlation with the number of bacteria. In the euphotic zone the phosphate/bacteria relation is positive from the surface down to 30–40 m, and negative below.

Marine bacteriologists ought to be grateful to Dr. Cviić for the comprehensive studies he has entered upon, and for presenting his paper in English. It is, however, a matter of regret that several errata and disagreements make it difficult to read.

O. M. Sømme

H. Kadota. "A study on the marine aerobic cellulose-decomposing bacteria". Mem. Coll. Agric. Kyoto Univ., **74**: 1–128, 4 figs. and 23 pl. Kyoto, 1956.

Fishing nets made from natural cellulose fibres, such as cotton, hemp, ramie etc., are in certain waters seriously damaged by cellulose-decomposing bacteria. It is estimated that in Japan about 75 per cent. of these nets have to be replaced annually. Investigations associated with this problem were carried out in Maizuru Bay and Hiroshima Bay in 1950–54. They include: isolation of pure cultures of aerobic cellulose-decomposing bacteria, identification of the species,

influence of ecological and physiological conditions, and prevention of the bacterial deterioration by means of modification of the cellulosic material or by chemical disinfectants.

Aerobic bacteria were found to be responsible for most of the damage of the cellulose fibres. The bacteria were widely distributed in the water and in bottom deposits, whereas anaerobic cellulose decomposers were not found in the water, and only sparsely in the mud. Two hundred and fifty-two pure cultures were isolated, belonging to 3 genera, 18 species, and 2 varieties. Fourteen new species were described by the author.

Experiments with cotton fishing nets submerged in the sea indicated that cellulose-decomposing bacteria accumulated on the yarns. This was especially characteristic for the *Cytophaga* group, which is otherwise difficult to isolate from sea water. To study the survival of bacteria during storing of the nets, samples of fishing nets were kept under wet or dry conditions after various periods in the sea. The number of viable bacteria was determined at intervals from 0 to 53 days. The actual number is not quoted, but the correlation between true bacteria and *Cytophaga* indicate that while true bacteria dominate on nets newly immersed in the sea, *Cytophaga* are responsible for most of the deterioration of stored nets.

The total number of cellulose-decomposing bacteria shows no definite seasonal fluctuations. Still, the fishing nets are more rapidly deteriorated in summer than in winter. This is due to the greater activity of the species of bacteria dominating during summer. They have a higher optimum temperature and a more rapid enzymatic breakdown of the cellulose molecule than the winter group of bacteria.

After describing the effect of temperature, pH, and salinity on the bacteria, some physiological and biochemical characteristics are recorded, for example, the various carbon and nitrogen sources that the different species are able to utilize. Of special interest are the experiments concerning the enzymatic breakdown of cellulose and cellulosic material. The results support the theory enounced by PRINGSHEIM and confirmed by several other bacteriologists, that the process is hydrolytic, in contrast to the "oxydative" decomposition maintained by WINOGRADSKY and others. The chemical breakdown of the cellulose molecule follows two ways, as found by STANIER. KADOTA was able to confirm that these two types of chemical decomposition correspond to two visually distinguishable types of maceration in attacked filter paper, viz., the "weathering" and the "liquefying" type.

Based on these observations, laboratory experiments were made to test the resistance of cellulose derivates towards cellulose decomposing bacteria. Samples of cellulose acetate with various contents of acetyl were exposed to pure cultures of 20 bacterial species. An acetyl content of 26·6–61·5 per cent. prohibited attack, a concentration corresponding to at least one acetyl group per anhydroglucose unit. The author indicates that "fishing nets made from cellulose acetate with acetyl contents at least 26,5 per cent will hardly rot either during immersion in the sea or during storage after fishing".

The cidal effect of chemical desinfectants was tested by adding various concentrations to pure cultures of living bacteria. The following compounds were employed: $CuSO_4$, $HgCl_2$, phenol, pentachlorphenol, 5-nitro-2-furfuryl semicarbazone, and cutch (a condensed tannin made from *Acacia catechu*). Among these chemicals $HgCl_2$ was the most effective, preventing growth of all

species in a concentration of 1:10,000, of most species at 1:100,000. Copper sulphate, which is widely used by Norwegian fishermen to preserve fishing nets, killed all organisms in a concentration of 1:1,000. Cutch, commonly used in Japan, even in a concentration of 1:100 killed only 10 of the 20 test organisms.

The practical application of these laboratory experiments was tested on ramie yarns immersed in the sea. The acetylated yarns with an acetyl content above 26·6 per cent. were completely resistant to bacterial attack. The only drawback with this material is that the tensile strength is somewhat reduced. This may be overcome if it is possible to find another cellulose derivate with stronger fibres.

Two of the desinfectants were tested on ramie yarn submerged in the sea, viz., $HgCl_2$ (1:10,000) and pentachlorphenol (1:2,000). The yarns were treated intermittently every 10 days for two hours. Nets impregnated in this way were estimated to last ten days longer than the untreated control, but the durability was far less than for the yarns made from 26·6 per cent. acetylated cellulose.

An account of previously described cellulose-decomposing bacteria is rendered in an appendix. The paper gives a thorough and comprehensive contribution to the knowledge of this bacterial group.

O. M. Sømme

G. Tregouboff et **M. Rose.** "Manuel de Planctonologie Méditerranéenne." Centre National de la Recherche Scientifique. Two vols, pp. 587, Pls. 207, Paris, 1957.

In 1924 JOHNSTONE, SCOTT, and CHADWICK produced their book on plankton, and this with STEUER's book of 1910 have been for many years, each in its own sphere, regarded as the general text books for planktologists. *Nordisches Plankton*, now unfortunately largely out of date, brought together into one series the knowledge of many experts so that other workers could the more easily identify their material. Since then our knowledge has increased, years of experience have been needed and many time-consuming hours have been spent in libraries searching out innumerable papers on particular subjects in scattered journals. These, with a few specialized books, have contained the data so urgently required by planktologists, young and old.

The International Council for the Exploration of the Sea was the first body to do something short and practical to relieve this problem with the start of the Plankton Identification Sheets in 1939 under the editorship of F. S. RUSSELL and Poul JESPERSEN. Each sheet in this series is written by a recognized authority on the subject and the series can be kept up to date, but production by this method takes time and is still continuing. Moreover, they apply largely to one area of the North Atlantic. A modern and reasonably comprehensive book on plankton, especially suitable for students has remained an unsatisfied need until very recently when in 1955 DAVIS attempted it for the American student in particular (see review by 'M.S.' in this Journal, **22** (2): 215–19). In 1956 HARDY produced his excellent book on the ecology of the living plankton. Now, dated 1957, we have another book, this time written especially for the student of plankton in the Mediterranean. These three books are quite different from each other, although there are similarities between this one and that by DAVIS.

In this new one TREGOUBOFF and ROSE have given their extensive knowledge

and experience for the benefit of others and the result is a pair of volumes, one of 587 pp. of text and one of 207 plates each with many figures, that will be regarded as a necessity for all libraries dealing in any way with the marine biology of the Mediterranean. It could also be a valuable addition to marine libraries outside this area, but its price of 7,500 francs means that few libraries could order it without serious consideration. It is, however, recommended for their consideration because it is unique in the way so much relevant information is brought together in a concise form. There are of course in other waters a vast number of species that are absent in the Mediterranean but although this needs to be remembered when following the keys, this book may well help the student and the research worker to be the more easily guided on the right lines, provided he knows when and where to look for further guidance.

The first three chapters deal briefly — very briefly — with the background information so valuable to the beginner who may find difficulty getting it in such a concise form elsewhere. The methods section is all too brief and deals only with those the student would be expected to use in the Mediterranean, not those in general use in the world's marine or fisheries laboratories. These three chapters together occupy only 32 pages leaving the other five hundred to the taxonomic groups. (Compare this conception with the 141 pages of introduction and 139 pages to the groups in DAVIS.) It was good to see "nanoplankton" spelled as such and not "nannoplankton" which seems in danger of becoming a commonly accepted mis-spelling.

There are 36 chapters on the various plankton groups starting with the Myxophyceae and ending with the Cephalochordata. These chapters are of varying length according to the importance of the group to the Mediterranean student of marine biology and to the available knowledge about it. Some are as short as a couple of pages, while diatoms take 30 and dinoflagellates 43 pages. To those outside the immediate sphere of intended readers some chapters seem rather out of proportion — e.g., 28 pages on Ciliates and only 36 on the whole of the Crustacea from Cladocera to Decapoda. Nevertheless on the whole these chapters are well conceived and contain information not given together elsewhere in such a form. Each is a simple review of our knowledge of the group, its general characters, anatomy, development, physiology, parasites, affinities, systematics, and methods of identification. Keys are usually clearly set out, and they are usually extended to species but sometimes only to genera (e.g., Copepoda). This part is then followed by a short but very useful section on practical hints for preservation.

Each of these chapters contains a list of works to be consulted, and these seem inadequate, omitting many works in general use in most laboratories, rather as though they referred only to those works readily available to the students at a small French Mediterranean library. The value of the book would be greatly enhanced by improved lists designed to help the reader find the extra data he wants with the minimum of time in searching card catalogues. Some examples — and these could be very many — of works that are not mentioned — include LEBOUR on diatoms and on dinoflagellates, GAARDER on coccolithophores and tintinnids, SEARS' review of the Abylidae and TOTTON on *Lensia*, SARS' Monaco report on Copepoda, W. and O. TATTERSALL on mysids. RUSSELL's monograph on the Medusae is included in the general chapter but is omitted from the list in the six chapters on the different orders of the Hydromedusae where it would have been of particular value. Reference

to the ICES plankton sheets seems very haphazard. The sections on planktonic larvae, especially the echinoderm and polychaete larvae will be very useful as the known data on these are very scattered. That on decapod larvae seemed a little disappointing.

Pelagic Cephalopoda are considered as nekton and are thus omitted, although they are often taken in plankton collections. There is much less excuse for the omission of a chapter on fish eggs and the planktonic stages of fish, and such a chapter would have been a much appreciated addition by the general student.

It is perhaps too much to expect that even such experienced experts as TREGOUBOFF and ROSE can be up to date on each of such a range of subjects, so that there are inevitably some such omissions and errors. One example occurs on p. 482 where *Sagitta planctonis* is mentioned from deep water. Since RITTER ZAHONY considered this to be synonymous with *S. zetesios* many of us have made this mistake but in 1956 DAVID showed that *S. zetesios* is a valid species and is the deep water form. There is no index in the usual sense but merely a contents list of chapters which is at the end of the book. References to a particular technique are sometimes given in the text, e.g. "la méthode de Bedot (1896)" but though the method may be fully described with comments on its use there is not always a reference included in the text to lead one to the original. The plates are produced as a separate volume in which, incidentally, there is a revised key for the Copepoda. The figures are mostly well produced, but why, oh why, is the full legend not given with each plate instead of only in a list at the end of the particular chapter in volume I? This may be convenient for the publisher but is certainly a great inconvenience for the reader for whom the book is written. Sometimes a plate is labelled only in very general terms, e.g. "Annélides Polychètes", and at other times more precisely labelled, but never in full giving details of the annotations. There are other eccentricities, e.g., plate 93 has a dozen figures annotated from 1–12, but plate 96 also with a dozen figures is cryptically annotated Pd. cu, I0. ph, Rh. fu, Ph. pi etc., and plate 160 has both types. Sometimes size is indicated on the figure and sometimes not.

If this review has stressed too much these items of criticism it is hoped that it will some day help in the production of an even better second edition, for there is much of value in this book. Its production has been no easy task and no volume of this sort is ever likely to satisfy all its readers. To repeat, it will be a necessity for all marine biological libraries dealing with the Mediterranean and it is recommended for serious consideration elsewhere according to the funds available.

J. H. Fraser

Current Bibliography

Prepared by A. R. MARGETTS

NOTE. The scope of the Bibliography is limited in the main to the area covered by the Council's activities, but there are included papers of general interest relating to other areas in North Temperate and Arctic regions and exceptionally elsewhere. Limnological references are not as a rule given but papers relating to brackish waters and to salmon and freshwater fish studied by the Council are included.

Subscribers and those on the distribution list will receive regularly upon application to the General Secretary copies of the Bibliography printed on one side of the page only, for use in making up card indices.

The Editor will be glad to be advised of emendations and additions to the Bibliography.

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